University of Alberta

Parasites of coral reef honeycomb groupers *Epinephelus merra* (Perciformes: Serranidae) from French Polynesia: patterns, processes, and taxonomy.

by

Mark Rigby ©

A thesis submitted to the Faculty of Graduate Studies and Research in partial fulfillment of the requirements for the degree of Master of Science.

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The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research for acceptance, a thesis entitled "Parasites of coral reef honeycomb grouper *Epinephelus merra* (Perciformes: Serranidae) from French Polynesia: patterns, processes, and taxonomy" submitted by **Mark C. Rigby** in partial fulfillment of the requirements for the degree of **Master of Science**. in Environmental Biology and Ecology.

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Abstract

Patterns in the gastrointestinal helminth fauna of honeycomb groupers *Epinephelus merra* (Perciformes: Serranidae) were investigated in French Polynesia. Their parasite faunae was found to be species poor, with no interactions among the helminths evident. Host habitat type was found to influence the parasite community and the parasite communities differed among islands from different archipelagos but not among islands in the same archipelago or among different sites on the same island. Larval honeycomb groupers were parasitized, and, with other fish larvae, may represent a means of dispersal for parasites. The decrease in digenean species diversity in honeycomb groupers and other serranids from west to east in the south Pacific was found to be positively related to fish diversity. The spirurid nematodes of French Polynesian coral reef-associated fishes are also described herein. There was no species cline in camallanid nematodes of fishes from west to east in the south Pacific.

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1. General Introduction

The spatial distribution of organisms is often heterogeneous, with their abundances related to discontinuities in environmental characters that produce areas of suitable habitat, or habitat patches. In a group of habitat patches, two types of processes affect population and community dynamics. The first includes interactions amongst organisms (of different or the same species) and amongst organisms and their habitat; the second involves movement of individuals and species among patches. The first set of interactions refers to within-patch dynamics, whereas the second refers to among-patch or metapopulation dynamics (see reviews by Hastings and Harrison 1994; Wu and Loucks 1995). Using this framework, organisms from individual patches may interact with each other to form patterns in the abundance and distribution of organisms either on 1) the scale at which individual organisms move and interact, generally within the same patch, or 2) the scale at which individuals infrequently move from one patch to another across unsuitable habitat. Because these interactions may depend on environmental conditions, patterns may also occur on larger scales, up to the scale of the zoogeographic species range (Hartvigsen and Halvorsen 1994). These patterns in abundance and distribution of organisms across nested and discontinuous hierarchies of habitat patches form ecological systems.

Just as individual organisms may interact with each other on different scales, individuals and communities of organisms may be affected by ecological processes operating at different scales. The ecological processes affecting communities operate at varied temporal and spatial scales (Weins 1989) to produce the observed patterns in species assemblages. Understanding these patterns in species assemblages, and the scales over which they occur, may be regarded as the central problem in ecology (Levin 1992). As the processes behind these patterns may operate at different scales, the scale at which a pattern is observed should provide insight into which process is responsible for that pattern. However, processes affecting communities may operate on different scales than those on which the patterns are observed, and patterns observed at any one scale may be due to the interactions of different ecological processes. Large scale patterns may be formed from a composite of multiple patterns at smaller scales, small scale patterns may be imposed by large scale constraints (Levin 1992), or the pattern may be due to a combination of large and small scale processes. As an example of small scale patterns determined by large scale constraints, Engle (1994) demonstrated that in the Southern California Channel Islands (USA), large scale oceanographic processes determine which subtidal marine species are present to interact with each other and produce patterns on smaller scales. If observations are made at only one scale, conclusions may be reached that do not apply, or are even contradictory, to other scales (Addicott et al. 1987). Therefore, integrating observations over different scales may help to elucidate which processes produce the observed patterns.

In ecological studies, the basic unit of scale may be difficult to determine. In many systems, the boundaries within which interactions among species occur may be vague as each species may have a different range, or functional patch size. However, host-parasite systems would seem to be ideally suited for the study of scale in ecology as the basic unit of scale, the host, is easily defined and discretely bounded. Direct interactions between parasites and their hosts, or among parasites, occur only within the individual host. Thus, the host is the field on which ecological interactions take place.

Within each scale, patterns in species assemblages may not be readily determined from the analysis of a single community. Reliably detecting recurrent patterns in natural communities requires the use of a system of communities that share a common pool of colonizing species. This required degree of replication may be found in host-parasite systems as a population of hosts furnishes replicated parasite communities, each of which is contained within an individual host (the infracommunity) and is recruited from a larger pool of species comprised of all the species found in all local host populations (the supracommunity) (Lotz and Font 1991).

When studying an infracommunity, the diversity of environmental variables that must be taken into consideration may be limited by examining only the gastrointestinal helminths within a host as 1) the environmental variables of the gastrointestinal tract are generally more predictable than that of the outer surface of the host, 2) many of these variables change along a linear gradient (i.e., that of the gastrointestinal tract) so that location within the gut encapsulates much of the environmental variation (Bush and Holmes 1986), and 3) parasites in the gastrointestinal tract have similar physiologies and life history strategies, making competition more likely and its study more amenable.

Gastrointestinal helminths of marine fishes generally have complex life cycles, requiring multiple hosts of different taxa to complete their development. Transfer between hosts is normally via ingestion with many intermediate stages lost to ecological sinks. The extent to which a parasite's life cycle, especially the transfer between hosts, is favored or hindered is a function of the ecological processes of the habitat in which the host resides. These processes may differ markedly for hosts of a species whose range extends across a variety of environments, potentially isolating hosts in one location from the parasites of hosts in another. Processes operating at large scales may determine which parasites are present to interact at smaller scales; e.g., the flow of large scale water currents carrying the copepod intermediate hosts of many marine helminths determine what areas may be colonized.

Aspects of ecological scale have been extensively studied among islands (see MacArthur and Wilson 1967; MacArthur 1972; Rosenzweig 1995). Islands, like hosts, are easily defined, replicated, and discretely bounded. Therefore, both islands and hosts are more amenable for the study of ecological problems than other areas where the boundaries of ecological interaction are vague and vary for each organism in the community. Although attention in the past has mostly been given to processes governing patterns in terrestrial island fauna, these same principles apply to the processes influencing reef-associated organisms, which have been examined to a lesser extent (e.g., Sale 1991, Engle 1994).

Most reef-associated organisms have pelagic larvae which, for the most part, disperse passively using oceanic currents. Some of these larvae may recruit locally, to either the same or nearby reefs (or habitat patches), whereas others may travel greater distances to other, and sometimes new, habitat patches. Mortality of larvae while in the pelagic phase is very high and larvae may remain pelagic for only a limited duration before they must recruit or die from starvation (Booth and Brosnan 1995). Therefore, for pelagic larvae, the difficulty in crossing inhospitable distances between habitat patches increases significantly with distance. This decreases the likelihood that reef organisms may colonize distant habitats. For island chains, such as those of the southern Pacific, larvae disperse from a source, or a mainland, community to colonize, either directly or via a series of stepping stones, habitat patches that are increasingly distant from the source community. In this situation, an inverse relationship between distance and species diversity of the colonized habitat patches would be expected (MacArthur and Wilson 1967). The source community for reef-associated organisms of the western and central Pacific is considered to be the coastal waters of Indonesia and northeastern Australia (Kay 1980; Springer 1982; Myers 1992). These organisms are thought to have dispersed north (to the Philippines and Japan), northeast (to the Marshall islands and Hawai'i), south (to the Great Barrier Reef and New Zealand), and southeast across the island chains of the southern Pacific (Myers 1992).

The islands of the southern Pacific are generally separated from each other by large distances (Sale 1991) and abyssal depths (Garth 1974), which are effective barriers for coral reef-associated organisms that cannot live in the pelagic environment or, usually, disperse across it as adults. These islands are spread over a large distances and offer a variety of environments. The coral reefs of French Polynesia provide an excellent opportunity for the use of spatial scaling in the study of the parasites of coral reef organisms. Coral reefs are composed of a number of different environments in close proximity that are easily distinguished from each other and have a large number of species to study. The ecology of French Polynesian coral reefs has been extensively studied for the past twenty years, and the flora and fauna of the coral reefs are relatively well known (see Delesalle et al. 1985). The ichthyofaunae of high islands are known to be more similar to each other than to those of atolls (Galzin 1987*a*), and the reef communities differ in species diversity and abundance with reef type (e.g., outer reef slope, barrier reef, fringing reef, and inner slope of atolls) (Galzin 1987*b*) due to differing environmental conditions.

However, the parasites of coral reef organisms remain relatively unstudied in French Polynesia. Indeed, the gastrointestinal parasites of reef-associated organisms of islands along the southeastern colonization route of the south Pacific have been studied in only a few locations to date, and in those locations, primarily the digeneans of fishes that have been studied; e.g., Australia (Lester and Sewell 1989; Cribb et al. 1994), New Caledonia (Manter 1969), and Fiji (Manter 1963; Amin and Nahhas 1994; Nahhas and Wetzel 1995). Therefore, to take advantage of the extensive body of knowledge on French Polynesian coral reefs, and the general lack of knowledge of the parasites of coral reef organisms in the southern central Pacific, our group (M. C. Rigby and Dr. J. C. Holmes of the University of Alberta and C. M. Lo, Drs. C. Combes, E. Faliex, and S. Morand of the Université de Perpignan) began a program on the parasites of coral reef fishes in French Polynesia.

In this thesis, I shall use 3 approaches to the study of spatial scale in the gastrointestinal helminth communities of reef fishes. **First**, I shall examine the patterns found in gastrointestinal helminth communities of a representative carnivorous reef fish, the honeycomb grouper *Epinephelus merra* (Perciformes: Serranidae), across multiple spatial scales. **Second**, I shall evaluate one of the possible means of dispersal of the parasites of reef fishes by examining larvae of *E. merra* as they recruit to the coral reef from the pelagic environment. **Lastly**, I will use a taxonomic approach to examine the distribution and possible means of dispersal of a common group of gastrointestinal helminths of coral reef fish, camallanid nematodes, from a variety of reef-associated fishes.

Honeycomb groupers were chosen for use in the study of spatial scales in the gastrointestinal helminth communities and for comparison with the work of Holmes (1990) on china rockfish *Sebastes nebulosus* (Scorpaeniformes: Scorpaenidae) of the northeast Pacific. The gastrointestinal helminth infracommunities of china rockfish are species rich, with large numbers of individual worms. In china rockfish, abundance and diversity of parasites reflect the degree of exposure of the reef to oceanic currents, parasite diversity may also be related to the diversity of related and other fishes on the same reef, a relatively large number of rarely occurring and a smaller number of nearly ubiquitous parasite species were found, and the ubiquitous species varied both in time and space (Holmes unpublished data). Comparing their helminth infracommunities with those of a similar fish in a different environment might allow for a better assessment of the factors determining infracommunity structure.

The parasite communities of honeycomb groupers may be compared to those of china rockfish as both fish are ecologically similar shallow-water species and are opportunistic “sit-and-wait” predators with a wide dietary range. Honeycomb groupers, like many serranids, are solitary site-attached fish that lay in wait beneath coral heads or in crevices during the day and more actively hunt their prey at night (Harmelin-Vivien and Bouchon 1976; Heemstra and Randall 1993). China rockfish are similar in that they are solitary territorial fish and wait in crevices in the reef for passing prey items (Love 1991). Honeycomb groupers prey upon shrimps, crabs, fishes, molluscs, stomatopods, and hermit crabs (Harmelin-Vivien and Bouchon 1976), while china rockfish prey upon crabs, brittle stars, other benthic prey of limited vagility, and fishes (Holmes 1990). The wide range of prey items, including many detritivores, such as crabs and various molluscs (which should be good accumulators of intermediate helminth stages), should expose both fishes to a variety of different parasites. Honeycomb groupers grow to a size of about 23 cm (Myers 1992) and, like many other coral reef fishes, should live approximately 10 years (Booth and Brosnan 1995); china rockfish are larger (reaching about 43 cm) of unknown life span, although other similar cold-water rockfishes live longer than 20 years (Phillips 1964). The greater size and probable longevity of china rockfish may give them a more species rich and numerous helminth community than honeycomb groupers.

Honeycomb groupers have an extensive geographic range, from the east coast of Africa in the western Indian Ocean to the Pitcairn Islands in the southeastern Pacific, and are common in shallow sheltered or protected waters (Myers 1992). The abundance and site attachment of honeycomb groupers allows fish from adjacent reefs and islands to be treated as separate communities. Comparisons may then be made among these communities for spatial studies on a smaller scale. Additionally, the wide distribution of this fish allows for comparisons among fish from different island groups and zoogeographic regions to examine larger scale patterns in the gastrointestinal helminth communities of honeycomb groupers. However, as this fish is only found in fringing and barrier reefs (and the lagoons of atolls), comparisons with the exposed outer slope of islands cannot be made.

Similar to most reef organisms, the parasites of coral reef organisms use dispersal stages to traverse the distance between habitat patches, or hosts. While some parasite propagules may not disperse over great distances, others may travel much farther to more distant, and sometimes previously uncolonized, habitats, both hosts and reefs. Planktonic invertebrates serve as one such means of dispersal for the parasites of reef organisms (Marcogliese 1995); parasites use planktonic invertebrates both as intermediate hosts and as dispersal agents. Some parasites use multiple intermediate hosts to complete their development and to place them at the appropriate trophic level to be consumed by their final, or definitive, host, usually a higher vertebrate, such as a coral reef fish. However, many of these fishes also have planktonic larvae. Thus, it may be possible for the parasites of adult fishes to infect the pelagic larvae of the fish for use as a means of dispersal for the parasites. *Epinephelus merra* is a mass recruiter, recruiting to the reef sporadically in very large numbers (Dufour unpublished observations). This provides an opportunity to obtain adequate sample sizes of fish recruits and follow-up samples of the same cohort of surviving juveniles from individual recruitment events.

One of the more widespread groups of gastrointestinal helminths of coral reef fishes in French Polynesia are camallanid nematodes (Morand et al. unpublished data), representing 66 % of nematode infections of fishes there (Rigby and Holmes 1996). The morphological affinities of the species found should help to show the relationships among them. From these relationships, and their relationships with other similar worms elsewhere, the degree of colonization versus local speciation may be determined. Additionally, once the taxonomy of these worms is known, the biology of similar worms may be used to help explain the ecological patterns seen in their definitive fish hosts; e.g., 1) the range of fish species infected, and what determines why a fish is infected, and 2) the number and type of intermediate hosts and how that affects the dispersal ability of the parasite.

I shall therefore explore the following topics to examine the spatial scales in the gastrointestinal helminths of the honeycomb grouper. In **chapter 2**, I cover the patterns found in the gastrointestinal helminth infracommunities of adult honeycomb groupers from islands across the southern Pacific and compare those patterns to the patterns observed by Holmes (1990) in china rockfish of the northeast Pacific. In **chapter 3**, I explore the possibility that parasites colonize islands using the pelagic larval stage of their definitive fish hosts by examining parasites of recruiting larvae and juvenile honeycomb groupers. In **chapter 4**, I examine the taxonomy of camallanid nematodes of a variety of coral reef fishes. Finally, in **chapter 5**, I provide a general discussion of the spatial scales observed in the parasites of fishes in the south Pacific.

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2. Patterns in the gastrointestinal helminths of a coral reef fish, *Epinephelus merra* (Serranidae), from French Polynesia and the South Pacific[1].

2.1. Introduction

With the concept of hierarchical spatial scales, ecologists have been able to better understand patterns observed in species assemblages, or communities (see general introduction above). Ecologists have thus been able to reconcile potentially conflicting patterns observed in the same communities at different scales (Wiens 1989) and obtain a more coherent picture of the processes structuring communities. Therefore, when possible, it is desirable to study communities using hierarchical spatial scales.

Parasite communities, for reasons given in the general introduction, are amenable to studies using spatial scale. Additionally, when the host has a wide geographic distribution, ecological patterns on larger spatial scales may also be investigated. Coral reef-associated fishes are a group that have a wide geographic distribution (e.g., Myers 1992) and a diverse parasite community (Cribb et al. 1994), making them suitable candidates for the study of parasite community structure at multiple spatial scales. To investigate spatial scales in parasite communities of coral reef-associated fishes, I have chosen a representative carnivorous fish, the honeycomb grouper *Epinephelus merra* (Perciformes: Serranidae).

Honeycomb groupers have a wide geographic distribution, from the east coast of Africa in the western Indian Ocean to the Pitcairn Islands in the southeastern Pacific (Heemstra and Randall 1993), which allows for large scale spatial studies of their parasite communities. Throughout much of the range of honeycomb groupers, there are many other closely related fishes (Myers 1992). These fishes should provide similar habitats to that of honeycomb groupers for gastrointestinal parasites and they may be used as hosts by some of the parasites of honeycomb groupers. Therefore, to understand the patterns found in the parasite communities of honeycomb groupers, these closely related fishes should also be investigated.

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[1] To be submitted, in part, as Rigby, M. C., Holmes, J. C., and Cribb, T. H. Patterns in the gastrointestinal helminths of a coral reef fish, *Epinephelus merra* (Serranidae), from French Polynesia and the South Pacific.

The diet of honeycomb groupers consists of shrimps, crabs, fishes, molluscs, stomatopods, and hermit crabs (Harmelin-Vivien and Bouchon 1976). This broad diet should expose them to a wide variety of gastrointestinal helminths and potentially give them a diverse parasite community. Honeycomb groupers are site-attached (Heemstra and Randall 1993) and common in shallow sheltered or protected waters (Myers 1992), thus increasing the ease with which collections may be made. As honeycomb groupers are site-attached, comparisons may be made between the parasite communities of fishes from fringing and barrier reefs (and the lagoons of atolls) of the same island and among nearby islands. However, comparisons cannot be made with the parasite communities from the outer slope as honeycomb groupers are not found there. Also, sex-related parasite patterns within this fish may not investigated as some individuals are intersex, i.e., containing both testicular and ovarian tissue within the gonads (Heemstra and Randall 1993).

I therefore investigated the patterns within the gastrointestinal helminth fauna of honeycomb groupers in the South Pacific on the following scales: 1) within individual fish, 2) within groups of fish taken from the same habitat, 3) between fish from different reef types or different locations on the same island, 4) between different islands within the same archipelago, 5) between islands in different archipelagos, and 6) over broader zoogeographic areas. Each of these scales addresses different questions. Do helminths interact within hosts? How predictable are infracommunities and does host-size affect the infracommunity? Does host habitat affect the infracommunity? Do parasite faunae vary between islands in the same archipelago? Do parasite faunae vary between archipelagos? Does gastrointestinal helminth diversity within honeycomb groupers decline from west to east in the Pacific as does fish diversity (Springer 1982)? Additionally, with the ecological similarities between honeycomb groupers and *Sebastes nebulosis* (Scorpaeniformes: Scorpaenidae) (see general introduction), it is possible to compare the processes influencing parasite community structure over various spatial scales between the 2 species.

2.2. Materials and Methods

The main study site was the high island of Moorea (Fig. 2-1B). Honeycomb groupers were sampled from the fringing (Fig. 2-1C: 2) and barrier reefs (Fig. 2-1C: 1) of Tiahura to examine the effect of reef type on the parasite community and from Vaipahu barrier reef (Fig. 2-1C: 3) to examine the influence of location (within the same island) on the parasite community. Fish were also sampled from two islands near Moorea, the atoll of Tetiaroa (the area sampled was barrier reef analogous to that of a high island) and the high island of Tahiti (Fig. 2-1B) (2 sites were sampled on Tahiti for representativeness; Taaone barrier reef [Fig. 2-1D: 1] and Taapuna barrier reef [Fig. 2-1D: 2]) to examine within island group patterns. For inter-archipelago comparisons, the fish from the above sampling area (Society Islands, Fig. 2-1B) were compared with fish sampled from the lagoons of the atolls of Rangiroa and Takapoto (Tuamotu archipelago, Fig. 2-1B). To investigate zoogeographic processes, fish from French Polynesia were compared to samples taken from Fiji (barrier reef of Suva Bay), New Caledonia, and Australia (Heron Island) (Fig. 2-1A).

Specimens were collected using a spear gun or line fishing. The total length and mass of each fish was measured. Fish were then eviscerated and the gastrointestinal tract was examined while fresh under a dissecting microscope. However, fish from Rangiroa, Tahiti, and Takapoto were frozen before examination and gastrointestinal tracts of fish from Tetiaroa were fixed in 70 % EtOH before examination. The gastrointestinal tract was divided into sections composed of the stomach, pyloric cecae, and five equal segments of the intestines. In fish from Australia, New Caledonia, and Tetiaroa, the intestines were not subdivided. Gastrointestinal helminths were provisionally identified, counted, their locations recorded, and fixed for later identification. Nematodes were fixed in hot 70 % EtOH, preserved in 70 % EtOH and 5 % glycerin, cleared in alcohol-glycerin-phenol and examined in temporary whole mounts in glycerin. Digeneans from French Polynesia and Fiji were heat killed, fixed in Bouin's fluid, dyed with Grenacher's alcoholic borax carmine, and mounted in Canada balsam for examination. Digeneans from New Caledonia and Australia were killed in hot 5 % formalin in sea water, dyed with Mayer's haemalum, and mounted in Canada balsam for examination.

Data on digeneans from Australian fishes (Heron Island) are from 1 *Epinephelus fasciatus* and 12 *Epinephelus quoyanus* (Serranidae) that I examined and from unpublished data on the digeneans of Heron Island from Dr. T. H. Cribb (University of Queensland). The digeneans known from honeycomb groupers in Heron Island are from 2 fish, 1 each examined by Drs. T. H. Cribb and R. M. Overstreet. On Heron Island's reef, digeneans appear to be the dominant group of gastrointestinal helminths with other adult helminth groups, including nematodes, appearing to be underrepresented (Cribb et al. 1994). Digeneans from New Caledonia were from 6 honeycomb groupers collected by Dr. S. Morand (Université de Perpignan) and examined by Drs. S. Morand and T. H. Cribb. Comparative data from *Cephalopholis argus* (Serranidae) from Moorea are from C. M. Lo (unpublished data).

Prevalence and mean intensity were defined as per Margolis *et al.* (1982). Differences in intensity were tested for significance using *t* tests and differences in prevalence using Fisher's exact test, with $P > 0.05$ considered non-significant. Due to the small sample size and low power of our analyses, corrections for multiple uses of the same data set were not performed in order to better recognize any patterns that may be present. Relationships between prevalence and host size were tested for significance using a G-test and relationships between intensity and host size were tested for significance using a linear regression. Positions for each helminth species along the gastrointestinal tract in each host were calculated using the methods in Bush and Holmes (1986). Data from hosts with single infections were compared to those from hosts with double infections using *t* tests.

Statistical analyses were performed using the programs in Systat v5.05 for Windows (Wilkinson et al. 1992).

2.3. Results

The gastrointestinal helminth faunae of honeycomb groupers in the Society islands were found to be species poor (3 species), with both low numbers of parasite species and individuals per host (Table 2-1). The digenean *Lecithochirium* sp. A was found within the stomach and rarely within the pyloric cecae, the juvenile cestode *Scolex polymorphus* occurred in both the pyloric cecae and the intestines, and the nematode *Spirocamallanus monotaxis* only within the intestines. The number of observed double infections of *Lecithochirium* sp. A with *Sp. monotaxis* (4) and with *Sc. polymorphus* (18) did not differ significantly from the number expected. There were 2 infections in which *Lecithochirium* sp. A was found within a caecum with *Sc. polymorphus*. The number of observed double infections (6) of *Sp. monotaxis* and *Sc. polymorphus* did not differ significantly from the number expected. No significant difference was found between the median positions of either parasite in single and double infections and both parasites occupied the same section of the intestines in 1 fish. Thus, there were no apparent interactions amongst these 3 species.

I pooled the data from fish from the Society Islands to look for size-related infection patterns. There were no differences in prevalence of any parasite when data from fish above and below median length of host were compared. No obvious significant relationship was seen between length of host and intensity of *Lecithochirium* sp. A or *Sp. monotaxis*. However, for *Sc. polymorphus* a significant positive relationship was found with host length (Fig. 2-2).

The fish of Tiahura barrier reef had more parasites (1.3 species and 12.8 individuals/fish) than those of Tiahura fringing reef (0.7 species and 2.8 individuals/fish)

(Table 2-1). *Lecithochirium* sp. A and *Sp. monotaxis* had significantly higher prevalences (Fisher's exact test, $P < 0.001$ and $P = 0.034$, respectively), but not intensities, on the barrier reef than on the fringing reef. *Scolex polymorphus* intensity was significantly higher (*t* test, $t = 2.13$, $P = 0.047$) on the barrier reef than on the fringing reef, but the prevalences were not significantly different. Fish from the barrier reef of Vaipahu had similar mean numbers of species (1.1) and worms per fish (8.1) to those of Tiahura barrier reef, and neither prevalence nor intensity of any of the 3 parasites were significantly different between Tiahura and Vaipahu barrier reefs. Similarly, prevalences of *Sp. monotaxis* and *Sc. polymorphus* were not significantly different between Taaone and Taapuna barrier reefs (despite the absence of *Sp. monotaxis* from Taaone). These patterns suggest that local variability has little effect on parasite assemblages. However, sample sizes were small and sample sites were not widely separated.

There was some evidence of differences among samples taken from different islands within the Society Islands. Though *Lecithochirium* sp. A was absent from both Tahiti and Tetiaroa, only its absence from Tahiti was significantly different from its prevalence on Moorea (Fisher's exact test, $P = 0.013$). The prevalence of *Sc. polymorphus* was also significantly higher on Moorea than on Tahiti or Tetiaroa (Fisher's exact test, $P = 0.0006$ and $P = 0.0009$, respectively), but did not differ between the last two. There were no differences in prevalence of *Sp. monotaxis* among Moorea, Tahiti, or Tetiaroa. Small sample sizes precluded tests of intensity data. Small sample sizes also hampered tests for differences between samples from Rangiroa and Takapoto in the Tuamotus; prevalences did not differ significantly despite the absence of *Lecithochirium* sp. B from Rangiroa and *Sc. polymorphus* from Takapoto.

There were distinct differences between gastrointestinal helminth parasites when samples are grouped into those from the Society Islands and those from the Tuamotus. Honeycomb groupers from both island groups shared *Sc. polymorphus*, although *Sc. polymorphus* was significantly less prevalent in the Tuamotus than the Societies (Fisher's exact test, $P < 0.0001$). Although honeycomb groupers from both island groups have digeneans and nematodes of the same families, Hemiuridae and Camallanidae, respectively, at about the same prevalences and intensities, the identities of those worms differ; *Lecithochirium* sp. A in the Society Islands was replaced by *Lecithochirium* sp. B in the Tuamotus and *Sp. monotaxis* in the Society Islands was replaced by *Camallanus marinus* in the Tuamotus (Table 2-1) even though *Sp. monotaxis* was found in other fishes in Rangiroa (see Chapter 4).

Samples of honeycomb groupers taken from islands further west show other differences. My samples from Fiji included two additional species of digeneans, and Manter (1961) reported a third (Table 2-2). Samples from New Caledonia included an additional digenean species and a trypanorhynch larva (Table 2-2). Small sample sizes, however, mean that the absence of *Lecithochirium* spp. or camallanid nematodes was not diagnostic. Honeycomb groupers are relatively rare at Heron Island, but I have records of 6 digenean species from 2 fish, plus an additional 2 species reported by Durio and Manter (1968) (Table 2-2). The presence or absence of parasites other than digeneans was not noted in fish sampled by others on Heron Island.

2.3.1. Other serranids examined

I examined small numbers of 2 other serranids, *Epinephelus fasciatus* and *Variola louti*, from Moorea. In addition, I examined 1 *E. fasciatus* and 12 *E. quoyanus*, a species closely related both ecologically and phylogenetically to honeycomb groupers, but slightly larger, from Heron Island. Unpublished comparative data on digeneans from these 3 species were also obtained from the records of Dr. T. H. Cribb. In each case, numbers of digenean species recorded from Heron Island were considerably greater than those from Moorea (Table 2-2). The number of digenean species from these fishes (Table 2-2), with additional unpublished data from Dr. T. H. Cribb on digeneans from *Diploprion bifasciatum*, *E. ongus*, and *Plectropomus leopardus* from Heron Island and data from Cedrik Lo from *Cephalopholis argus* from Moorea, are significantly related to the diversity of the fish faunae for each island (the number of expected reef fish families, from Springer 1982) (Fig. 2-3).

2.4. Discussion

Gastrointestinal parasite communities of French Polynesian honeycomb groupers were marked by a paucity of species that occurred both infrequently and in low numbers. The gastrointestinal parasite communities of other marine teleostean fishes are generally much richer (Holmes 1990; Curran and Caira 1995), with those of honeycomb groupers bearing more resemblance to the poorly developed freshwater fish parasite communities (Holmes 1990) (Fig. 2-4). This paucity of parasites made answering the questions posed in the introduction very difficult, as only very strong patterns could be detected.

2.4.1. Do helminths interact within hosts?

Similar to free living organisms, parasites have been shown to interact in several ways within the host environment. For gastrointestinal helminths the most common form of interaction is competition (Holmes 1973), although positive interactions (facilitation) are known. For example, both Shostak and Dick (1986) and Stock and Holmes (1987) showed that different kinds of very large tapeworms may produce intestinal damage which has a positive effect on some nematodes, presumably by increasing cell debris on which the nematodes feed. Although interactions may be shown by a variety of means, Bush and Holmes (1986) concluded that, in field data, altered distribution patterns were the most diagnostic, with competition revealed by displacement of one or more species and facilitation by attraction to the same location.

For these direct interactions to occur, 2, or more, organisms (or species) must occupy the same habitat patch (the host), and usually, the same site within the host. The evidence does not support either of these forms of interaction among the gastrointestinal helminths of honeycomb groupers from Moorea. While *Spirocamallanus monotaxis* overlapped in distribution with *Scolex polymorphus* in distribution within the host, there was no evidence of either displacement or attraction. Also, both parasites are from different feeding guilds (blood feeders [Fusco 1978] vs. absorbers), decreasing the likelihood of competition. *Lecithochirium* sp. A and *Sc. polymorphus* also overlapped in distribution within the host but, again, there was no evidence of displacement or attraction and both parasites were again from different feeding guilds (ingesters vs. absorbers). As there was no evidence of interaction among any of the parasites, their distributions may be better explained by independent site selection (Price 1980; Rohde 1979).

2.4.2. *How predictable are infracommunities and does host-size affect the infracommunity?*

Larger habitat patches are usually able to support more species rich communities with a greater number of individuals than smaller habitat patches (Rosenzweig 1995). This should also apply to host-parasite systems, where larger hosts not only offer more habitat space and may therefore support a larger parasite community, but also eat more, and may therefore be exposed to more parasites. In host-parasite systems, larger host body size is often positively correlated with species richness (Poulin 1995), and both prevalence and intensity are usually positively correlated with age in fish (Polyanski 1961), which may be used as a general indicator of size.

Among adult honeycomb groupers from Moorea, neither parasite species diversity nor prevalence increased with host size. Intensity, however, was positively related to host size for *Scolex polymorphus*, but not for the other parasites. *Scolex polymorphus* appears to be both common and widespread in fishes examined from Moorea (in at least 30 fish species [S. Morand et al. unpublished data]), more so than either of the other 2 parasites found in honeycomb groupers (*Sp. monotaxis* was found in 12 fish species of 8 families [see Chapter 4]; *Lecithochirium* sp. A. was found only in honeycomb groupers with unidentified worms of the same genus found in lionfishes [Rigby unpublished data]). As honeycomb groupers may acquire *Sc. polymorphus* by eating infected invertebrates or smaller forage fishes, their primary prey items (Harmelin-Vivien and Bouchon 1976), they should be repeatedly exposed to *Sc. polymorphus*. Also, larger fish should consume more prey items and, therefore, be exposed to a greater number of *Sc. polymorphus*, potentially leading to a higher parasite burden.

The only component of the honeycomb grouper parasite community that would therefore appear to be predictable is that *Sc. polymorphus* intensity should be greater in larger, and presumably older, fish. The other parasites neither occur predictably nor have predictable intensities within the same habitat patch. This lack of patterns within the helminth community of honeycomb groupers in French Polynesia is similar to that observed by Kennedy (1990) in freshwater fishes.

2.4.3. Does host habitat affect the infracommunity?

Host species may travel between, or their species range may extend across, the boundaries of larger habitat patches separated by physical characters that may serve as barriers to the means of dispersal used by parasites. However, suitable intermediate hosts may not be found in some habitats. In some habitats, the community structure of potential definitive hosts may not be able to support the parasite; e.g., an important host may be absent, or the population density of suitable hosts may be too low to support a viable parasite population (Holmes et al. 1977). Therefore, hosts from different habitats may be exposed to different parasites. This phenomenon should be more pronounced in site-attached host species, such as honeycomb groupers, that, generally, do not move between neighboring habitat patches and are therefore exposed only to the pool of parasite infective stages found in their habitat patch. For example, Aho et al. (1991) found that parasite communities varied considerably among different bowfin populations in North America. In bowfin, processes determining the abundance of host generalists (e.g., availability of suitable intermediate hosts, geographic location, or composition of the host community) strongly influenced the diversity of the parasite community.

Coral reef communities differ in fish community structure, current patterns, and invertebrate faunae, even between nearby habitats (e.g., Tiahura and Vaipahu barrier reefs [Galzin and Pointier 1985; Galzin 1987]). Differences in invertebrate faunae and current patterns may influence the local success of life cycles in helminths and, therefore, the rate of local extinction. In honeycomb groupers from Moorea, parasite communities from fishes from different but similar habitats (e.g., Tiahura and Vaipahu barrier reefs) were not significantly different. However, parasite communities from fishes from dissimilar habitats on the same island (e.g., barrier and fringing reefs of Tiahura) did differ (Table 2-1). The lower productivity of the fringing reef (Heatwole 1981) may also lower the size and density of both intermediate and definitive hosts for these parasites, thus, lowering the abundances of the parasites. Additionally, all of these parasites use copepods and other zooplankton as intermediate hosts (Stromberg and Crites 1973; Williams and Jones 1994; Marcogliese 1995). With the high level of water movement on the reefs of Moorea (residence time is 6h in Tiahura lagoon [Delesalle and Sournia 1992]), most infected zooplankton would presumably be borne onto the reef via oceanic currents over the barrier reef. There, however, the density of zooplankton is greatly reduced by the planktivorous fishes associated with the reef, or the "wall of mouths" of Doherty and Sale (1986). This would reduce the number of infective stages from the pelagic environment that reach the fringing reef and may contribute to the difference in parasite abundance observed.

2.4.4. Do parasite faunae vary between islands in the same archipelago?

Islands close together, in the same archipelago, and in the same oceanic current system should have similar reef-associated faunae. The 3 Society (and 2 Tuamotu) islands sampled were close together, in the same archipelago (Fig. 2-1: B), were in the same oceanic currents (see Planes 1993*a*), have similar coral reef-associated faunae (see Delesalle et al. 1985), and fish communities in the same archipelago are known to be more similar to each other than to islands in nearby archipelagos (Galzin 1987). Therefore, they are also likely to have more similar parasite faunae. Though sample sizes were small, the parasite faunae of Rangiroa and Takapoto in the Tuamotus were similar and the parasite faunae of Tahiti and Tetiaroa in the Society Islands were similar. However, in the Society Islands, Moorea had a higher prevalence of *Lecithochirium* sp. A than Tahiti and a higher prevalence of *Sc. polymorphus* than Tahiti or Tetiaroa. This may, in part, be due to the influence of local conditions for the sites sampled as 1) heavy fishing pressure on Tahiti has lowered fish populations and reduced the size of adult fishes and 2) siltation has lowered habitat quality (i.e., there is less live coral and more algae) on both Tahiti and Tetiaroa (personal observations). These 2 factors may lower the population size of both intermediate and definitive hosts, thus potentially reducing parasite populations. Dobson (1990) suggests that host population size is positively correlated with species diversity. With lower host population sizes, less abundant and, potentially, more specialized parasites should disappear from the host population. In my data, it appears that the more specialized parasite (*Lecithochirium* sp. A) may not be supported by the smaller host populations on Tahiti and Tetiaroa while the more general parasites (*Sc. polymorphus* and *Sp. monotaxis*) were retained. Therefore, it would appear that among the islands sampled within the same archipelago, helminth communities are similar but may be influenced by local conditions particular to the sites sampled.

2.4.5. Do parasite faunae vary between archipelagos?

The 2 archipelagos sampled here represent 2 groups of habitat patches separated from each other by a large geographic distance (250+ km) and opposing oceanic currents (see Planes 1993*a*). These factors appear to be significant enough to affect the dispersal of coral reef-associated organisms between the 2 archipelagos, producing differences in fish and mollusc faunae (Randall 1985; Richard 1985) and genetic differences in some of the fishes present in both archipelagos (e.g., Planes 1993*a*,*b*).

With these faunal differences, differences in the parasite communities of fishes from the 2 archipelagos would not be unexpected. For honeycomb groupers, it appears that the *Sp. monotaxis* present in the Society Islands is replaced by *Camallanus marinus* (both Nematoda: Camallanidae) and that one species of *Lecithochirium* replaces another (Table 2-1). For both groups of parasites, these differences may result, in part, from the differences in oceanic currents which may carry different pools of infective stages. For *Lecithochirium* spp., the difference in the mollusc faunae between the 2 archipelagos may prove more important, as digeneans are usually very specific for their mollusc first intermediate host (Williams and Jones 1994). Thus, *Lecithochirium* sp. A may be prevented from establishing in the Tuamotus if the necessary mollusc is absent.

The situation appears to be more complex among the camallanid nematodes. Their only necessary intermediate hosts are copepods (Stromberg and Crites 1973), and those nematodes that have been studied have a low specificity for their copepod hosts (Moravec et al. 1995). Thus, the absence of a suitable intermediate host is unlikely to restrict these nematodes. However, honeycomb groupers are not known to consume copepods (Harmelin-Vivien and Bouchon 1976), and the absence of the necessary paratenic host (or, the the intermediate host that serves as a trophic bridge between copepods and honeycomb groupers) may restrict the parasite's host distribution. In addition, *Sp. monotaxis* was present in other fishes in the Tuamotus (see Chapter 4). Though a potential competitor was found in honeycomb groupers from the Tuamotus (*Camallanus marinus*, which should also be a blood feeder as are other similar worms [Meguid and Eure 1996]), it is doubtful that *Sp. monotaxis* has been competitively excluded from honeycomb groupers as both prevalence and intensity of *C. marinus* were low, leaving many unoccupied habitat patches available.

2.4.6. Does gastrointestinal helminth diversity within honeycomb groupers decline from west to east in the Pacific as does fish diversity (Springer 1982)?

The degree of isolation, or distance, of an island from a "mainland" is, for many organisms, inversely correlated with immigration rate and, therefore, species diversity (MacArthur and Wilson 1967; Rosenzweig 1995). For the reef-associated organisms of the southern Pacific, the coastal waters of Indonesia and northeastern Australia serve as the mainland, or the area of greatest species diversity, from which the islands of the south Pacific are thought to have been colonized (Myers 1992). Across the south Pacific, from west to east, habitat patches for reef-associated organisms (islands), become more widely dispersed and smaller, thus reducing the number of "stepping stones" as well. This makes colonization and immigration to these islands progressively more difficult as distance from the mainland increases. The increasing difficulty in colonization has produced a number of clines in the species diversity of reef-associated organisms from west to east in the south Pacific: echinoderms, corals, molluscs (Kay 1980), and fishes (Springer 1982; Myers

1992). The diversity of digeneans found within honeycomb groupers, and other serranids, was also found to decrease from west to east (Fig. 2-3). This pattern may be due to the increasing difficulty in colonization, or to the decrease in availability and diversity of suitable definitive host species (serranid fishes) or the molluscan intermediate hosts from west to east across the south Pacific.

2.4.7. How do these patterns compare with those observed in china rockfish of the northeastern Pacific?

The parasite community of china rockfish was found to be considerably richer, including a relatively large number (22) of rarely occurring and a smaller number (5) of nearly ubiquitous parasite species (Holmes 1990). The parasite community of honeycomb groupers of Moorea contained only 1 nearly ubiquitous species, *Sc. polymorphus*, and 2 more rarely occurring species, *Sp. monotaxis* and *Lecithochirium* sp. A. The richer parasite community of china rockfish allows patterns to be detected with relative ease; the poorly developed parasite community in honeycomb groupers allows only gross differences in presence of species to be noted. In this regard, the parasite community of honeycomb groupers appears to be similar to those of freshwater fishes in which species diversity and abundances are usually low (Fig. 2-4). Additionally, china rockfish were not investigated over the larger scales used in my investigation of honeycomb groupers.

The richer parasite community of china rockfish may result from their greater size and closer proximity to their heartland. Larger fish are expected to eat more and, therefore, be exposed to more parasites; however, the disadvantage of smaller size for honeycomb groupers would be expected to be offset by the faster digestion rates, and hence increased feeding rates, at the higher water temperatures. Larger fish, however, can eat larger prey, which may be more effective accumulators of larval helminths. Overall, size may be expected to account for a minor part of the differences.

China rockfish were sampled near the area with the greatest diversity of closely related species (Eschmeyer et al. 1983), or their heartland. This should also be the area of greatest parasite species diversity, with parasite diversity negatively related to distance from the host species' heartland (Kennedy and Bush 1994). French Polynesia is near the eastern edge of the range of the honeycomb grouper (Heemstra and Randall 1993) and the heartland for similar epinepheline species appears to be near Indonesia/northeastern Australia (based on distributions given in Heemstra and Randall 1993). The records of parasites of honeycomb groupers, and other closely related serranids, sampled across the Pacific (Table 2-2) show that digenean species diversity is negatively related to distance from the heartland of honeycomb groupers (Fig. 2-3). Additionally, the greatest community richness in honeycomb groupers was found closest to the heartland (New Caledonia; quantitative data from Heron Island was not available) and that of a closely related fish, *Epinephelus quoyanus*, from near the heartland (Heron Island) should estimate community richness in honeycomb groupers there as well (Fig. 2-4), supporting Kennedy and Bush's (1994) suggestion.

The abundance and diversity of parasites in china rockfish was strongly correlated with the degree of wave exposure (and, thus, the diversity of benthic faunae) of the reef from which they were taken (Holmes unpublished data). The greater abundance of parasites observed in honeycomb groupers from the barrier reefs rather than the fringing reefs of Moorea may reflect the same pattern.

Parasite diversity in china rockfish also appears to be related to the diversity of other fishes, especially congeners, on the same reef. Different host species there have high populations of parasite species that occur in lower numbers in other host species, such as china rockfish (Holmes unpublished data). Although fish community composition between reefs sampled on Moorea did differ (Tiahura has a different community than Vaipahu barrier reef [Galzin 1987]), there was no significant difference in the parasite communities of honeycomb groupers. However, on a larger scale, this same pattern was seen from west to east across the south Pacific in the parasite communities of honeycomb groupers. This "exchange" of parasites may be the mechanism producing the pattern of greater parasite diversity near the heartland.

Table 2-1. Gastrointestinal helminths collected from honeycomb groupers *Epinephelus merra* in French Polynesia by collection site. Data are prevalence, mean intensity ± standard deviation.

				Mean number of parasite			
	Reef type	Date (mo/yr)	Sample size	species/ fish	individuals/ fish	*Lecithochirium* sp. A	*Lecithochirium* sp. B
Society Islands							
Moorea							
Tiahura	barrier	5/94; 1,4,5/95	41	1.27	12.85	39, 2.3 ± 1.7	
Tiahura	fringing	2,4,5/95	33	0.7	2.76	3, 1	
Vaipahu	barrier	1,4,5/95	30	1.13	8.13	30, 1.3 ± 0.5	
sum			104	1.05	8.29	25, 1.9 ± 1.4	
Tahiti							
Taaone	barrier	2/95	10	0.30	0.60		
Taapuna	barrier	2-3/95	9	0.44	1.56		
sum			19	0.37	1.05		
Tetiaroa	barrier	6/95	10	0.20	0.30		
Tuamotu Islands							
Rangiroa	lagoon	3/95	12	0.33	2.50		
Takapoto	lagoon	3/95	20	0.25	0.25		10, 1

Table 2-1. Continued.

	Reef type	*Spirocamallanus monotaxis*	*Camallanus marinus*	*Scolex polymorphus*
Society Islands				
Moorea				
Tiahura	barrier	27, 3.7 ± 3.8		61, 18 ± 30
Tiahura	fringing	6, 1		61, 4.4 ± 4.1
Vaipahu	barrier	7, 1.5 ± 0.7		77, 10 ± 15.8
sum		14, 3.1 ± 3.4		65, 11.3 ± 21
Tahiti				
Taaone	barrier			30, 2 ± 1
Taapuna	barrier	33, 4.3 ± 5.8		11, 1
sum		16, 4.3 ± 5.8		21, 1.8 ± 1
Tetiaroa	barrier	10, 2		10, 1
Tuamotu Islands				
Rangiroa	lagoon		25, 1	8, 27
Takapoto	lagoon		15, 1	

Table 2-2. Gastrointestinal helminths found in serranids from the south Pacific by sampling location. Data are parasite, prevalence, mean intensity.

	Heron Island	New Caledonia	Fiji
Epinephelus merra	n = 2	n = 8	n = 10
	Bivesicula claviformis[c] 50	*Helicometra fasciata* 75, 3.5	*Bivesicula claviformis*[e]
	Cainocreadium epinepheli[b, c] 50	*Lepidapedoides kerapu* 25, 1	*Helicometra fasciata* 40, 3.8
	Helicomtra fasciata[a, b] 50	*Scolex polymorphus* 13, 1	immature *Lecithaster* sp. 10, 1
	Lepidapedoides kerapu[a] 50	trypanorhynch larvae 13, 5	*Scolex polymorphus* 40, 3.3
	Pacificreadium serrani[d]		
	Prosorhynchus sp. 1.[c] 50		
	Prosorhynchus sp. 2.[c] 50		
	Pseudoplagioporus interruptus[d]		
Epinephelus fasciatus	n = 21		
	Acanthocolpids 5, 1.0		
	Allopodocyle epinepheli[a] 5		
	Rivesicula claviformis[a] 14		
	Helicometra fasciata[a,b] 81		
	Lecithochirium sp.[a] 5		
	Lepidapedoides kerapu[a] 14		
	Scolex polymorphus 5		
Epinephelus quoyanus	n = 12		
	Acanthocephala 8, 1		
	Allopodocotyle epinepheli 58, 7.4		
	Ascarophis sp. 83, 14.3		
	Bivesicula claviformis 33, 1.5		
	Bucephalids 92, 32.8		
	Cainocreadium epinepheli 17, 1.5		
	Helicometra fasciata 17, 1		
	Lecithochirium sp. 33		
	Lepidapedoides kerapu 17, 9.5		
	Scolex polymorphus 100		
Variola louti	n = 1		
	Bucephalids[a] 100		
	Pleurus digitatus[a] 100		
	Prosorhynchus sp. A.[a] 100		
	Prosorhynchus sp. B.[a] 100		
	Prosorhynchus sp. C.[a] 100		

Note: [a] = Cribb unpublished data, [b] = Bray and Cribb (1989), [c] = Overstreet *in litt*, [d] = Durio and Manter (1968), [e] = Manter (1961).

Table 2-2. Continued.

	Society Islands	Tuamotu Islands
Epinephelus merra	n = 133	n = 32
	Lecithochirium sp. A. 20, 1.9	*Camallanus marinus* 19, 1
	Scolex polymorphus 53, 10.6	*Lecithochirium* sp. B. 6, 1
	Spirocamallanus monotaxis 14, 3.2	*Scolex polymorphus* 3, 27
Epinephelus fasciatus	n = 5	
	Bivesicula sp. 100, 7.6	
Epinephelus quoyanus		
Variola louti	n = 5	n = 2
	Scolex polymorphus 100	*Scolex polymorphus* 100, 2
	Spirocamallanus sp. 20, 1	

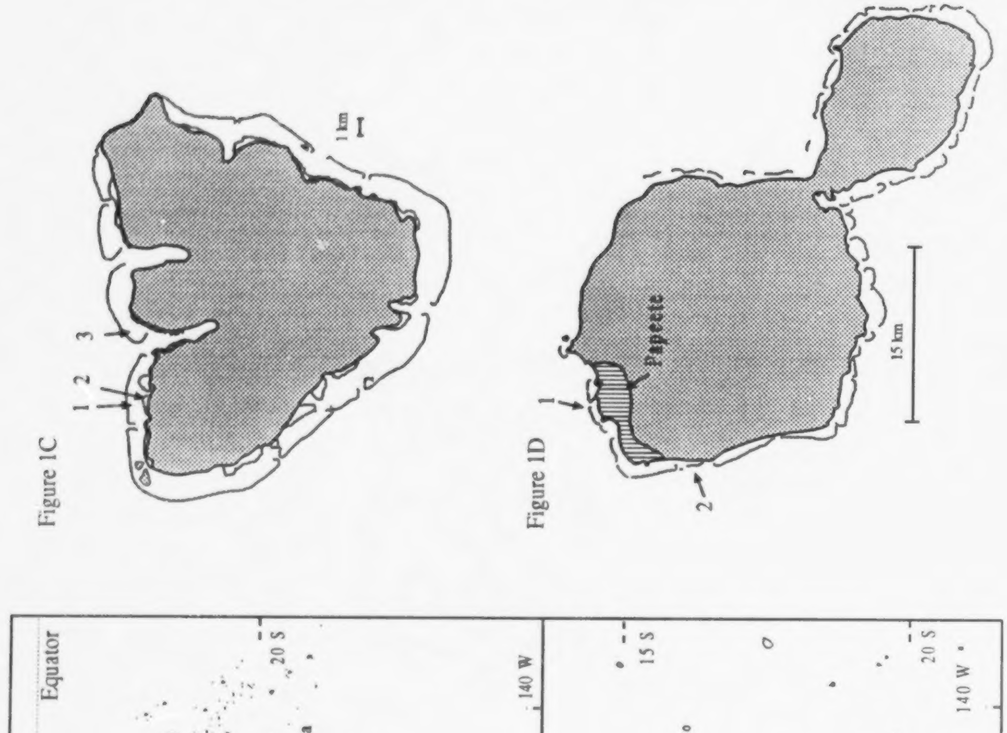
Figure 1A
Equator
French
Polynesia
Fiji
New Caledonia
Heron Island
140 E
160 E
180
160 W
140 W
20 S
Figure 1B
Tuamotus
Takapoto
Rangiroa
Tetiaroa
Tahiti
Moorea
Society Islands
500 km
150 W
140 W
15 S
20 S
Figure 1C
1
2
3
1 km
Figure 1D
Papeete
1
2
15 km

Fig. 2-1. Sampling areas in A) the South Pacific, B) French Polynesia (solid islands represent high volcanic islands and open islands represent atolls), C) Moorea, reefs shown in outline (1 = Tiahura barrier reef, 2 = Tiahura fringing reef, 3 = Vaipahu barrier reef), and D) Tahiti, capital city, Papeete, shown with vertical stripes and reefs shown in outline (1 = Taaone barrier reef, 2 = Taapuna barrier reef).

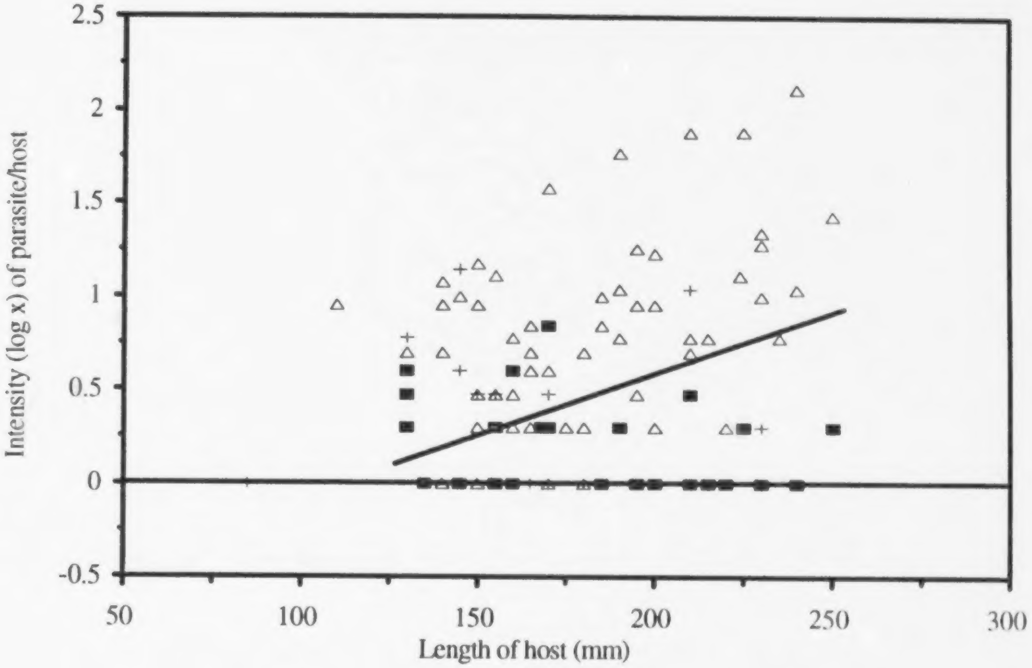

Fig. 2-2. Influence of size on parasite intensity in honeycomb groupers (zeroes excluded) for the Society Islands. Closed squares (■) represent *Lecithochirium* sp. A, crosses (+) represent *Spirocamallanus monotaxis*, and open triangles (Δ) represent *Scolex polymorphus*. Solid line shows linear regression of intensity (log x) of *Scolex polymorphus* per host ($y = 0.0054x - 0.1716$, $r^2 = 0.16$, $p = 0.0003$).

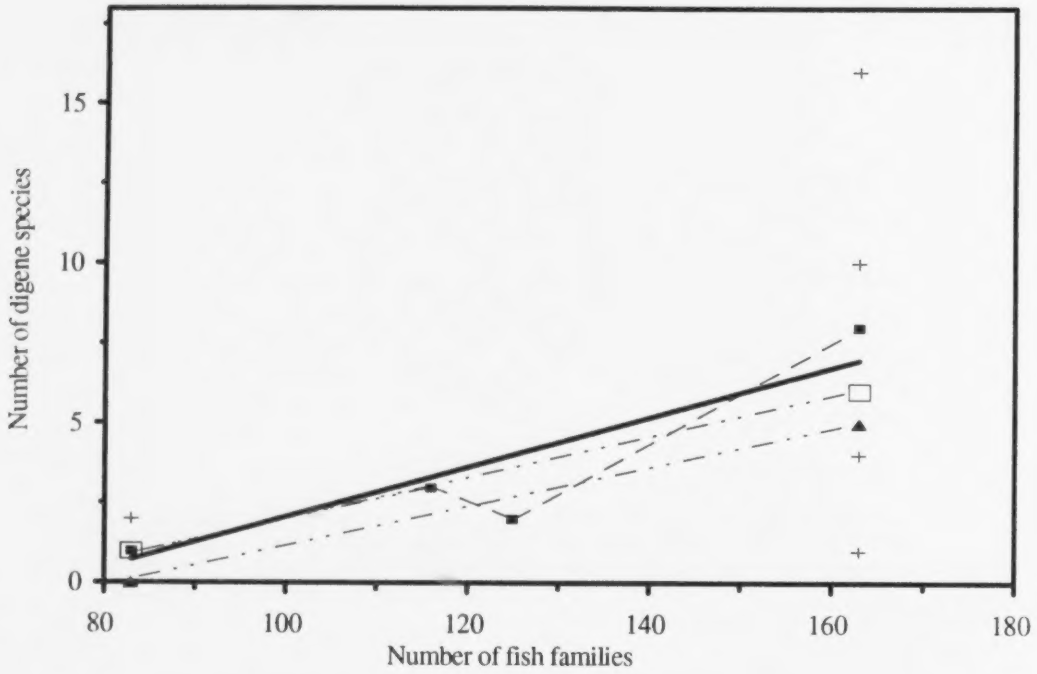

Fig. 2-3. Influence of fish diversity on numbers of digenean species known from serranids in Moorea, Fiji, New Caledonia, and Heron Island. Thick line shows linear regression of number of digeneans per location ($y = 0.078x - 5.77$; $r^2 = 0.35$, $p = 0.019$). Thin lines connect same host species from each location. Closed squares (■) represent honeycomb groupers, open squares (□) represent *E. fasciatus*, closed triangles (▲) represent *Variola louti*, and crosses (+) represent other serranids (see text for species).

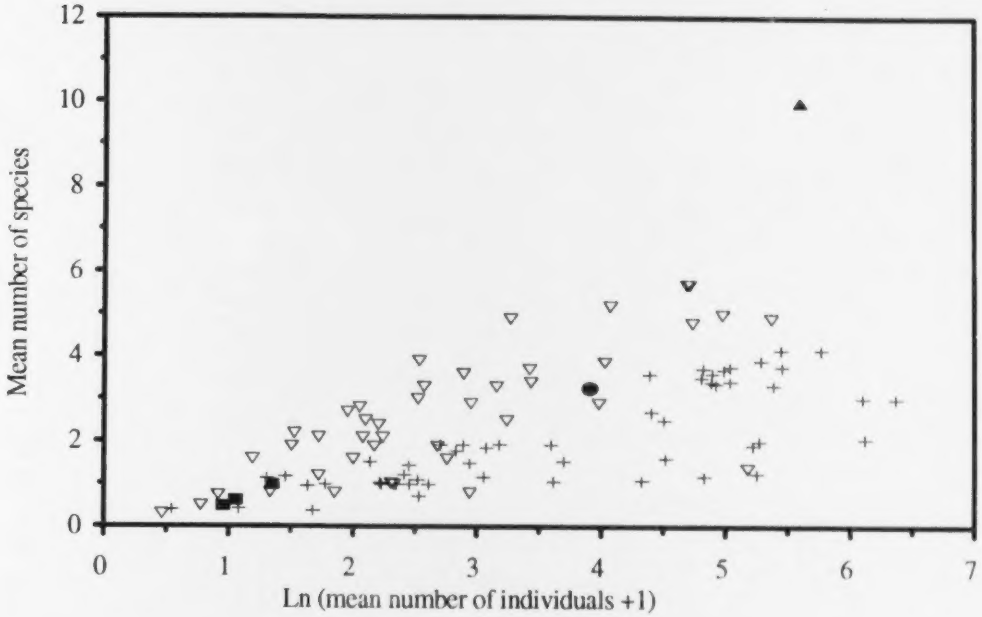

Fig. 2-4. Community richness of adult gastrointestinal helminths of marine fishes (∇) in comparison with those of freshwater fishes (+). Closed squares (■) represents honeycomb groupers from Tiahura barrier reef Moorea, Fiji, and New Caledonia (from left to right). Closed circle (•) represents *Epinephelus quoyanus* sampled from Heron Island, Australia. Closed triangle (▲) represents china rockfish. Data from china rockfish and other fishes from Holmes (1990).

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3. Parasites of coral reef fish recruits, *Epinephelus merra* (Serranidae), in French Polynesia[1].

3.1. Introduction

Although there has been an increasing amount of work done on the parasites of adult coral reef fishes (Hasegawa et al. 1991; Cribb et al. 1994; Nahhas and Wetzel 1995), virtually no attention has been paid to the parasites of larval and pre-settlement coral reef fishes (for parasites of larval marine fishes, see Polyanski 1961; Rosenthal 1967; Wojciechowska 1993). To my knowledge, the only report of parasites of larval and pre-settlement coral reef fishes is that of the hydrozoan *Hydrichthys* sp. on transforming convict surgeonfish (*Acanthurus triostegus sandvicensis*) in Hawaii (Randall 1961). This parasitic form of *Hydrichthys* has also been observed on several species of Acanthuridae, including the convict surgeonfish in French Polynesia (Dufour and Rigby unpublished observations). Fitness of adult fishes may be appreciably affected by parasitism (see references in Adlard and Lester 1994; Williams and Jones 1994). Pelagic fish larvae and recruiting fishes have a very steep survival curve (Victor 1986; Shulman and Ogden 1987; Booth 1995). As predation significantly reduces the number of settlement stage and younger fishes (Shulman and Ogden 1987; Hixon 1991; Carr and Hixon 1995), even a slight decrease in fitness may be expected to lead to differential mortality. Therefore, I would expect that the additional stress of parasitism in fish larvae, with the much greater parasite to host size ratio, would cause differential mortality in larval fish hosts. Indeed, there is ample evidence for differential mortality of fish larvae in freshwater systems (see references in Williams and Jones 1994). The dynamics of larval fishes should play a major role in determining the structure and stability of adult populations (Sale 1980; Victor 1986) because even slight variations in survivorship during the early recruitment phase of fishes may produce substantial variations in adult population size (Doherty and Williams 1988; Doherty and Fowler 1994).

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[1] Published as Rigby, M. C., and Dufour, V. 1996. Parasites of coral reef fish recruits, *Epinephelus merra* (Serranidae), in French Polynesia. Journal of Parasitology **82**: 405-408.

During spawning, the eggs of some coral reef fishes are released into the open ocean, where they drift with oceanic currents. The eggs then hatch and the larvae remain in the pelagic environment until they have attained a size suitable for recruitment back to the coral reef (Leis 1991). While pelagic, larvae consume microzooplankton (Leis 1991), some of which are intermediate hosts for a number of helminth parasites of fishes (Marcogliese 1995). Larvae of the honeycomb grouper *Epinephelus merra* (Serranidae) follow this pattern but primarily recruit to the lagoons of coral reefs in very large schools over a 1 - 2 day period. These large scale recruitment events occur infrequently for the fishes of this family (Dufour and Galzin 1993; Dufour unpublished observations). Two recruitment events of the honeycomb grouper were observed during a 2 mo study period in Moorea island, French Polynesia, in 1995. I examined fixed honeycomb grouper recruits captured from these 2 events to determine whether or not parasitism influenced the recruitment and subsequent survival of larvae. Here, I report on the internal helminth parasites found and examine the possibility of parasite-induced differential mortality in reef fishes recruits.

3.2. Materials and Methods

Fish were captured during colonization to the lagoon in 4 crest nets (mouth size 0.75 X 2 m, 1 mm mesh size) set overnight in the surf zone on the outer reef crest of Moorea island. French Polynesia (17°30' S, 149°50' W) (Fig. 3-1). Nets were emptied each morning and left in place every night throughout the study period (30 January to 29 March 1995). Specimens were preserved in 5 % formalin in sea water before examination and identified according to the descriptions in Leis and Rennis (1983) and Leis and Trnski (1989). Recruits from the second, and larger, recruitment event, along with some sub-adults and adults, were sampled using rotenone 1.5 mo after settlement on the fringing reef of the south coast. Juvenile fish were fixed in 70 % ethanol; sub-adults and adults were frozen before examination. Adult fishes were collected using a spear gun from the fringing and barrier reefs of the north coast of the island and examined fresh. Total fish lengths were determined to the nearest millimeter. All fish were eviscerated and the gastrointestinal tracts, including the associated mesenteries, were examined for internal parasites under a dissecting microscope. Parasites were cleared in glycerin and examined as wet mounts. Voucher specimens were deposited in the United States National Parasite Collection (USNPC accession numbers 85874 and 85875, for trypanorhynchs and phyllobothriids, respectively).

Differences in prevalence were tested for significance using Fisher's exact test and differences in intensity were tested for significance using a *t* - test. Both tests were performed using the programs in Systat v5.05 for Windows.

3.3. Results

Two recruitment events of honeycomb groupers were observed. Each event took place over a 1 night period, centered on 1 sampling location, with small numbers caught in the adjacent sampling sites. The first event occurred on 9 February 1995 (1,296 recruits captured at A, Fig. 3-1) on the west coast; the second event occurred on 9 March 1995 (4,437 captured at B, Fig. 3-1) on the south coast. Less than a total of 100 recruits per day for all 4 nets were captured for the rest of the study period. Honeycomb grouper recruits were infected with opaque white trypanorhynch blastocysts and phyllobothriid metacestodes, encysted on the outside of the gastrointestinal tract (Table 3-1). No recruits from either event were simultaneously infected with both types of parasites and only 2 fish from the second event had more than 1 parasite (2 phyllobothriids in each). Prevalences of trypanorhynchs (Fisher's exact test, $P = 0.0287$) and phyllobothriids (Fisher's exact test, $P = 0.0002$) were significantly higher in the second recruitment event. There was no significant difference between the sizes of infected and uninfected fish recruits within a recruitment event ($t = 1.309$, $P = 0.321$; $t = 0.0768$, $P = 0.9390$, respectively) but fish from the second event were larger ($t = 4.007$, $P = 0.0001$) (Table 3-1).

On 21 April 1995, juvenile, sub-adult, and adult honeycomb groupers were captured using rotenone on the south coast fringing reef (site B, Fig. 3-1) (Table 3-1). There were no double infections in juvenile fish sampled. Trypanorhynch blastocysts and phyllobothriid metacestodes recovered from juveniles were brown. Prevalences of trypanorhynchs (Fisher's exact test, $P = 0.4332$) and phyllobothriids (Fisher's exact test, $P = 0.7248$) were not significantly different in juvenile fish than in recruits from the second event, but were significantly greater than in fish from the first recruitment event (Fisher's exact test, $P = 0.0337$; Fisher's exact test, $P = 0.0081$, respectively). The mean total length of juvenile fish was significantly greater than that of fish from the second event ($t = 3.853$, $P = 0.0016$) (Table 3-1). Infected fish did not differ in length from uninfected fish ($t = 0.143$, $P = 0.892$).

Trypanorhynch blastocysts found within sub-adults were brown. Prevalence of trypanorhynch blastocysts was not significantly different from any of the preceding size classes sampled at this site (Fisher's exact test, $P = 0.5943$, $P = 0.5161$, $P = 0.3164$, respectively). Phyllobothriids were not found in sub-adults, which is significantly different from juveniles sampled (Fisher's exact test, $P = 0.0324$).

Neither of the above parasites was found in adult honeycomb groupers sampled from the south coast. However, this is not statistically different from the low prevalence of trypanorhynch blastocysts in sub-adults (Fisher's exact test, $P = 0.5174$). Over a one year period, 117 honeycomb groupers were sampled from reefs on the north coast of Moorea with no trypanorhynch blastocysts or phyllobothriids found. Thus, no trypanorhynch blastocysts were found in 137 adults sampled from Moorea, significantly lower than the number found in sub-adults (Fisher's exact test, $P = 0.0349$). However, with such a sample size, either parasite may still be present, but at a maximum prevalence of 2.16 % (Post and Millest 1991).

3.4. Discussion

The general pattern observed was that both trypanorhynch blastocysts and phyllobothriid metacestodes were present in recruits and absent in larger and older fish. Polyanski (1961) reported a similar pattern in mullets, with their "childhood parasites" gradually disappearing and being replaced by the typical parasites of adult fishes. From this distribution of internal parasites by length, or age, of host, I postulate 3 explanations: (1.) differential mortality acts upon infected fish, eventually eliminating them from the population; (2.) both parasites represent recent introductions to the area; and (3.) parasites are eliminated by the host.

If differential predation was to occur, I would expect to see it operate upon recruits, which already have a lower survival rate, rather than on sub-adults and adults (Hixon 1991). Many parasites adversely affect their hosts, or modify host behavior, to increase the host's vulnerability to predation and enhance the parasite's transmission to definitive hosts (Holmes and Zohar 1990; Poulin 1995), such that hosts are differentially preyed upon. Larval trypanorhynchs, such as those studied here, have been implicated in parasite-induced host mortality (Sakanari and Moser 1990). One indicator of whether or not parasite-induced mortality occurs within a host population is to observe a decrease in parasite prevalence with increasing host age (Lester 1984). As prevalences of both parasites were statistically unchanged from recruits to juvenile fish for both parasites and from juveniles to sub-adults for trypanorhynchs, the data do not support the hypothesis of differential predation upon infected post-settlement hosts as the main factor in explaining the eventual elimination of these parasites from their hosts.

Both hosts and their parasites may be colonists. Coral reefs in the south Pacific, including the archipelago containing Moorea (the Society Islands), represent patchy habitats that are geographically remote from other suitable habitats for coral reef fishes and initial colonization may be difficult not only for fishes, but also for their parasites.

Larval serranids, including honeycomb groupers, recruit from the pelagic environment to their adult habitat (Leis 1987). Where the larvae that settled on Moorea originated and by what oceanic route they traveled to Moorea is completely unknown. Pelagic larval fishes may represent an important dispersal mechanism for parasites, allowing parasites to colonize new reef environments. However, it appears unlikely that the parasites found here in honeycomb grouper recruits, but not adults, represent novel infections. First, although neither parasite has been identified, both belong to parasitic groups that are wide spread and common in elasmobranchs (Williams and Jones 1994). Many different elasmobranchs, both reef and pelagic, are known to be present in the Society Islands (Randall 1985). Second, the only elasmobranch I examined, a lemon shark *Negaprion acutidens*, had both trypanorhynch and phyllobothriid adults (C. M. Lo and M. C. Rigby unpublished observations). Third, trypanorhynch blastocysts were found in sub-adults from the south coast which came from a different and earlier recruitment event than the juveniles. Fourth, both parasites were found in other adult fishes (C. M. Lo and M. C. Rigby unpublished observations). Therefore, similar, if not the same, parasites were already present on the island. Though I cannot rule out the possibility that fish larvae may be used to bring these larval parasites from the pelagic environment into the reef and complete the parasite's life cycle, it appears unlikely that the parasites found in honeycomb grouper recruits were colonizing this island for the first time.

Although I have not followed the parasites within the same cohort of fish throughout its development and have used hosts from different recruitment events (i.e., juveniles, sub-adults, and adults from the south coast are all from separate recruitment events and all adults are not necessarily from a single event), I believe they may be treated as members of the same population, as all recruit to Moorea, where they will probably join the same reproductive pool, from the surrounding ocean, where they may be exposed to both parasites. This is illustrated by the presence of both parasites in recruits from both recruitment events and the presence of trypanorhynchs in sub-adults.

The distribution pattern of both parasites within honeycomb groupers is perhaps best explained by their destruction by a developing immune response. While I have not identified the pigment responsible for the discoloration of parasites in older fish, I will refer to them as being "melanized". Here, "melanization" appears to begin after settlement, with trypanorhynchs eliminated from hosts by the adult stage and phyllobothriids eliminated by the sub-adult stage. Because I examined only fixed or frozen hosts, I do not know whether or not the "melanized" parasites were alive. However, I consider this "melanization" to be evidence of a host-initiated immune response that isolates and kills the parasite. During their pelagic phase, when mortality of fish larvae is high (Leis 1991), selective pressure should favor individual responses, such as colonization at night (Dufour 1991) or swimming ability (Stobustki and Bellwood 1994) or fast growth curves, which lower mortality. Therefore, little energy should be devoted to immune responses. After settlement, selective pressures should change such that energy may be devoted to immune responses. It appears most likely that neither parasite is acquired by the host after settlement and, thereafter, a prolonged immune response starts which eventually eliminates the parasites from the host via "melanization".

It would seem unlikely that any larvae present in such small fish would reach their definitive elasmobranch hosts directly unless small sharks prey upon the dense schools of larvae. However, for other immature cestodes, e.g., *Diphyllobothrium* plerocercoids (Dick and Choudhury 1995), trophic transfer from an intermediate host to a paratenic host is possible. Metacestodes found in honeycomb grouper recruits may be passed on via trophic transfer to larger pelagic or reef fishes (before the parasites are killed) and, eventually, to elasmobranchs. Thus, honeycomb groupers do not necessarily represent an ecological sink for either parasite.

Although it seems unlikely that either parasite caused differential mortality in settlement stage fish, they may be more important in earlier, pelagic, developmental stages. Adamson and Caira (1994) state that intermediate stages of parasites using their hosts as trophic channels may enter a state of minimal interaction with their hosts, minimizing pathogenicity. However, such a non-pathogenic relationship may occur only after the parasites have encysted within the host. Assuming developmental patterns of trypanorhynchs as in Sakanari and Moser (1985), considerable development of these trypanorhynchs within the fish larvae is necessary before encystment. Energy for development may be taken from the host, lowering host fitness, and leading to parasite-induced mortality. This may take the form of greater sensitivity to starvation, lower swimming efficiency, or lower predator avoidance abilities. It is more likely that differential mortality would operate upon pelagic larvae while the parasites are still developing, rather than in recruits in which the parasites were encysted. Therefore, further study of the effects of parasites on pre-settlement honeycomb groupers and both pre- and post-settlement fishes of other species is needed.

Table 3-1. Body cavity parasites of honeycomb groupers from Moorea.

				Trypanorhynch blastocysts		Phyllobothriid metacestodes	
Age group	Collection Date	Mean TL ± S.E.	Sample size	Preva-lence (%)	Mean intensity	Preva-lence (%)	Mean intensity ± S.E.
1st recruits	9 Feb.	33.7 ± 1.14	100	3	1.0	1	1.0
2nd recruits	9 March	34.7 ± 1.43	100	12	1.0	16	1.1 ± 0.09
juveniles	21 April	38.8 ± 1.32	16	19	1.0	19	1.0
sub-adults	21 April	93.0 ± 3.83	32	6	1.0	-	-
adults	21 April	189.3 ± 4.97	20	-	-	-	-

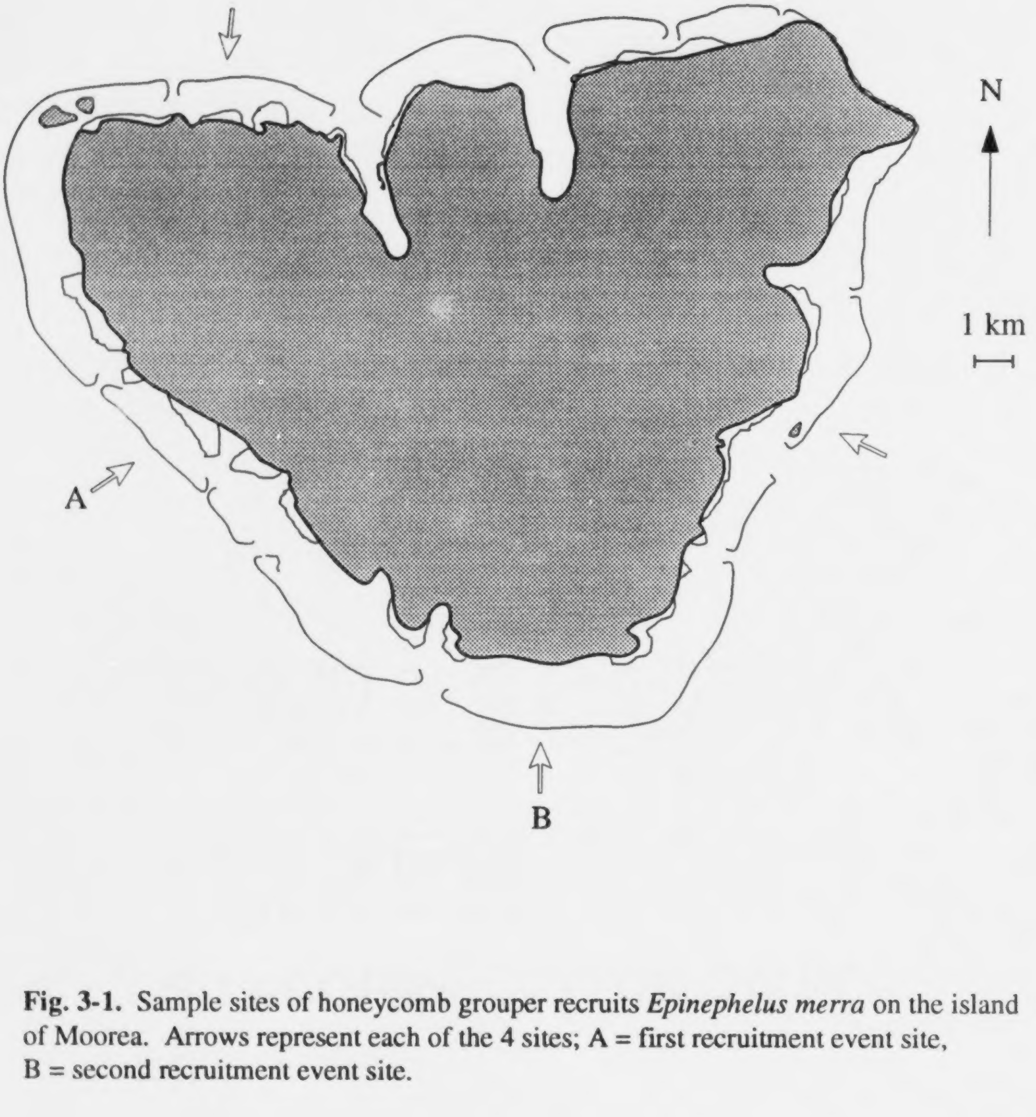

Fig. 3-1. Sample sites of honeycomb grouper recruits *Epinephelus merra* on the island of Moorea. Arrows represent each of the 4 sites; A = first recruitment event site, B = second recruitment event site.

3.5. References

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4. Nematodes of French Polynesian coral reef fishes. Families Philometridae and Camallanidae[1].

4.1. Introduction

Although the coral reefs of French Polynesia have been well studied (e.g., Delesalle et al. 1985), the parasite faunae of coral reef associated organisms there have been neglected until recently. As part of investigations of the parasites of the honeycomb grouper, *Epinephelus merra* (Serranidae), in the south Pacific and the biodiversity of coral reef fish parasites in French Polynesia, nematodes were collected from coral reef fishes from Moorea in the Society Islands (17°30' S, 149°50' W) and Rangiroa in the Tuamotu Islands (15° 10' S, 147° 40' W). Among the nematodes recovered from fishes were an immature female philometrid and 5 additional species of camallanids. *Spirocamallanus istiblenni* Noble, 1966, *Spirocamallanus monotaxis* Olsen, 1952 and *Camallanus marinus* Schmidt and Kuntz, 1969 are redescribed and 2 new species of *Spirocamallanus*, *S. chaimha* n. sp. and *S. colei* n. sp., are described from material from French Polynesia.

4.2. Materials and Methods

Nematodes from Moorea and Rangiroa were killed in hot 70 % EtOH, and stored in 70 % EtOH and 5 % glycerin, those from Hawai'i were killed in Berland's fluid (9 parts glacial acetic acid: 1 part 100 % formalin) and stored in 70 % EtOH and 5 % glycerin, and those from Fiji were heat killed in Bouin's fluid and stored in 70 % EtOH. All nematodes were examined as temporary whole mounts in glycerin after clearing in alcohol-glycerin-phenol. Drawings were made using a drawing tube and final illustrations were prepared using with Adobe Illustrator™. Measurements given are means and standard deviations followed by ranges in parentheses. All measurements are in µm.

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[1] Part of this chapter has been submitted as 1) Rigby, M. C., and Font, W. F. Redescription and Range Extension of *Spirocamallanus istiblenni* Noble, 1966 (Nematoda: Camallanidae) from Coral Reef Fishes in the Pacific. submitted to the Journal of the Helminthological Society of Washington. and part will be submitted as 2) Rigby, M. C., and Adamson, M. L. Nematodes of French Polynesian coral reef fishes. Families Philometridae and Camallanidae. submitted to the Canadian Journal of Zoology.

Specimens of the following species were examined for comparative purposes: (1) *Spirocamallanus istiblenni* Noble, 1966 (1 male and 1 female, United States National Parasite Collection (USNPC) accession numbers 72590 and 72591, respectively) from *Istiblennius zebra* in Hawaii and from *Bothus pantherinus, Parapercis cylindrica, Parapercis polythalma,* and *Plectorhynchus picus* in Okinawa, Japan (4 males and 4 females, USNPC 81816; 1 male, USNPC 81817; 1 male, USNPC 81818; and 4 males, USNPC 81819, respectively), (2) *Spirocamallanus monotaxis* Olsen, 1952 (1 male and 1 female, USNPC 37251) from *Monotaxis grandoculis* in Hawai'i, (3) *Camallanus marinus* Schmidt and Kuntz, 1969 (5 males and 2 females, USNPC 71398) from *Trichiurus haumela* in the Philippines, and (4) *Spirocamallanus guttatusi* (Machida and Taki, 1985) (2 males, National Science Museum, Tokyo (NSMT) accession number 1802) from *Siganus guttatus* in the Philippines. Type specimens of *Camallanus atropusi* Bashirullah and Khan, 1973, *C. dollfusi* Bashirullah and Khan, 1973, *C. chauhani* Srivastava and Gupta, 1975, *C. puriensis* Srivastava and Gupta, 1975, *C. therapsi* Srivastava and Gupta, 1975, *C. pentkotai* Srivastava and Gupta, 1976, *C. trichiurisi* Srivastava and Gupta, 1976, and *C. trichiuris* Bashirullah and Rahman, 1972 could not be located for examination.

4.3. Species descriptions

4.3.1. ***Philometra*** sp. (immature female) Fig. 4-1

General

Nematoda, Spirurida, Dracunculoidea, Philometridae, *Philometra*. Translucent red in life. Apparently sexually immature females. Cuticle thin and nonstriated. Cephalic and cervical papillae (anterior deirids) not seen. Esophagus with anterior swelling. Excretory pore not seen.

Female (2 immature specimens)

Length 82,752 ± 27,247 (63,486-102,019). Anterior region swollen, maximum width 675 ± 66 (628-722). Maximum width at midbody 652 ± 45 (602-684). Length of esophagus 952 ± 68 (904-1000). Nerve ring 185 ± 64 (139-230) from apex. Anterior flexure of ovary ends 302 ± 72 (252-353) from apex and posterior extremity of anterior ovary ends 1,445 ± 559 (1,050-1,840) from apex. Amphidelphic; anterior ovary directed anteriorly, curved around esophagus, posterior ovary recurved and ending 382 ± 268 (192-572) from posterior extremity. Eggs and larvae absent. Anus (1 specimen) 374 from posterior extremity. Tail simple, without spine-like projections (mucrons), rounded.

Host: *Epinephelus merra* Bloch, 1790 (Perciformes, Serranidae).
Site in host: peritoneal cavity.
Prevalence: 1 % (2/192)
Mean intensity: 1.0
Locality: barrier reef of Moorea, Society Islands, French Polynesia.
Date of Collection: May, 1995.
Specimens deposited: USNPC XXXXX and French National Museum of Natural History XXXX.

Remarks

I cannot identify this material to species in the absence of sexually mature specimens. Superficially similar sexually immature specimens were recovered by Cedrik Lo of the Université de Perpignan from the body cavities of *Cephalopholis argus* (Serranidae) and *Stegastes nigricans* (Pomacanthidae) but were not examined. The low prevalence and lack of sexually mature worms suggest accidental infections. Addionally, 1 markedly different adult female philometrid was found that will be described elsewhere as a new genus and species in collaboration with Dr. Martin Adamson.

4.3.2. ***Camallanus marinus*** Schmidt and Kuntz, 1969 Fig. 4-2

Synonyms: *C. trichiuris* Bashirullah and Rahman, 1972 n. syn., *C. atropusi* Bashirullah and Khan, 1973 n. syn., and *C. dollfusi* Bashirullah and Khan, 1973 n. syn.

General

Nematoda, Spirurida, Camallanoidea, Camallanidae, Camallaninae, *Camallanus*. Translucent red in life. Cuticle annulated. Mouth surrounded by 4 large papillae, 2 on each valve of buccal capsule. Buccal capsule laterally compressed, composed of three parts (2 valves and a basal ring), width and length subequal. Valves marked internally by interrupted longitudinal ridges, ridges more interrupted posteriorly. Longitudinal ridges most numerous near anterior margin of buccal capsule. Buccal valves supported by lateral tridents on each side, consisting of three posteriorly directed prongs extending beyond the basal ring, central prong longest. Tridents attached to buccal capsule by means of an anteriorly directed and divided process supporting each valve. Amphids not seen. Basal ring of buccal capsule connected to muscular esophagus by a prominent non-cuticularized cylinder. Nerve ring near posterior end of tridents. Esophagus long and slender; anterior muscular portion clearly divided from posterior glandular portion, muscular portion generally longer. Cervical papillae (anterior deirids) not observed. Excretory pore in region of posterior third of muscular esophagus. Tail simple, without spine-like projections (mucrons), gradually tapering to a point.

Male (2 complete specimens, 1 partial specimen)

Length 4,952 and 6,310, maximum width near midbody 219 ± 14 (203-230). Buccal capsule 144 ± 7 (140-152) long, including ring at base 17 ± 3 (15-20) long, 154 ± 5 (149-159) wide. Buccal capsule with 53 ± 3 (50-56) longitudinal ridges at anterior margin, 26 ± 2 (24-27) at widest portion, 8 ± 1 (7-9) ridges at base. Central prong of tridents 114 ± 12 (102-106) long. Muscular esophagus 1,002 ± 146 (905-1,170) long, glandular esophagus 812 ± 172 (614-914) long, ratio 1.26 ± 0.22 (1.03-1.47). Nerve ring 217 ± 11 (203-224) from apex. Excretory pore (1 specimen) 973 from apex. Anterior flexure of testis 976 and 1,620 from apex. Anus 73 and 99 from posterior extremity. Alae well developed, extend 342 and 427 from posterior extremity. Caudal papillae 13; 7 preanal pedunculate papillae, 2 adanal pedunculate papillae not attached to alae, 4 postanal papillae. Preanal papillae evenly spaced. First 2 postanal papillae grouped. Phasmids lateral, approximately two thirds of distance from posteriormost papillae to posterior extremity. Spicule single, simple, gradually tapers to a point, 238 and 248 long.

Female (2 complete specimens, 1 partial specimen)
Length 6,788 and 7,548, maximum width near midbody 269 ± 14 (254-282). Buccal capsule 166 ± 6 (162-173) long, including ring at base 21 ± 2 (19-23) long, 173 ± 18 (162-194) wide. Buccal capsule with 51 ± 6 (48-58) longitudinal ridges at anterior margin, 27 ± 3 (24-29) at widest portion, 7 ± 2 (6-9) ridges at base. Central prong of tridents 130 ± 7 (123-138) long. Muscular esophagus 1,180 ± 74 (1,097-1,233) long, glandular esophagus 1,145 ± 164 (996-1,320) long, ratio 1.05 ± 0.2 (0.83-1.22). Nerve ring 235 ± 24 (208-250) from apex. Excretory pore 853 and 1,175 from apex. Vulva 3,243 ± 762 (2,463-3,986) from apex. Vagina muscular, posteriorly directed from vulva. Uterus amphidelphic, eggs, but no larvae, in utero. Anus 79 and 178 from posterior extremity. Phasmids lateral, midway between anus and posterior extremity.

Host: *Epinephelus merra* Bloch, 1790 (Perciformes, Serranidae).
Locality: lagoons of Rangiroa and Takapoto, Tuamotu Islands, French Polynesia.
Date of Collection: March, 1995.
Site in host: intestines.
Prevalence: 30 % (6/20)
Mean intensity: 1.0
Specimens deposited: USNPC XXXXX and French National Museum of Natural History XXXX.
Previously reported: 1) Philippines from *Caranx affinis* (Perciformes, Carangidae), *Gazza minuta* (Leiognathidae), *Trichiurus haumela* (Trichiuridae), and *Thysanophrys nematophthalmus* (Scorpaeniformes, Platycephalidae) (see Schmidt and Kuntz 1969); 2) Bangladesh as

C. atropusi from *Trichiurus savala* (Perciformes, Trichiuridae) (see Bashirullah and Rahman 1972), as *C. atropusi* from *Atropus atropus* (Carangidae), and as *C. dollfusi* from *Trichiurus haumela* (Trichiuridae) (see Bashirullah and Khan 1973).

Remarks

The presence of a dorso-ventrally compressed sclerotized buccal capsule with longitudinal ridges, a basal ring but without a buccal capsule divided into anterior and posterior portions, and tridents place these worms within the genus *Camallanus*. Twelve species of *Camallanus* have been reported from marine fishes of the Indo-Pacific with a single spicule: *C. marinus* Schmidt and Kuntz, 1969, *C. chorinemi* Rasheed, 1970, *C. surmai* Rahseed, 1970, *C. atropusi* Bashirullah and Khan, 1973, *C. dollfusi* Bashirullah and Khan, 1973, *C. aotea* Slankis and Korotaeva, 1974, *C. chauhani* Srivastava and Gupta, 1975, *C. puriensis* Srivastava and Gupta, 1975, *C. therapsi* Srivastava and Gupta, 1975, *C. pentkotai* Srivastava and Gupta, 1976, *C. trichiurisi* Srivastava and Gupta, 1976, and *C. longimonospicula* Paruchin, 1978. In addition, Bashirullah and Rahman (1972) described *C. trichiuris* with 2 spicules but illustrated it with only 1. Although the present material is much smaller than *C. marinus*, it resembles *C. marinus* in number and arrangement of caudal and cephalic papillae, number of spicules, relative position of the vulva and nerve ring, shape of the buccal capsule, the pattern of longitudinal ridges lining the buccal capsule, and shape of the tridents (Table 4-1). Based on this suite of morphological similarities, I assign my specimens to *Camallanus marinus* Schmidt and Kuntz, 1969.

This material cannot be distinguished morphologically from the descriptions or figures of *C. atropusi*, *C. dollfusi*, and *C. trichiuris*. All 3 species have the same suite of characters that I am using to characterize *C. marinus*, and are distinguished only by minor differences (Table 4-1) and I regard these 3 worms as synonyms of *C. marinus*. This material may be distinguished from *C. chorinemi* by the absence of cervical papillae and the lack of a bifurcated spicule tip (both present in *C. chorinemi*). This material may be distinguished from the description of *C. surmai* by the presence of interrupted longitudinal ridges lining the buccal capsule (uninterrupted in *C. surmai*), the shorter length of the alae (342-427 vs. 940-1,000), and the absence of cervical papillae and a bifurcated spicule tip (both present in *C. surmai*). This material may be distinguished from *C. aotea* by the number of preanal (7 vs. 6) and postanal (4 vs. 7) papillae and by the shape of the buccal capsule (tridents shorter, basal ring less prominent, and non-cuticularized cylinder connecting basal ring to esophagus less prominent than in *C. aotea*). The buccal capsule morphology of *C. aotea* bears a strong resemblance to *Oncophora* but differs in the distribution of ridges lining the buccal capsule (most ridges continuous vs. anterior group of continuous ridges and a posterior group of spines). The diagnostic characteristics of *Oncophora* may, therefore, need to be reexamined. This material may be distinguished from *C. chauhani*, *C. pentkotai*, *C. puriensis*, *C. therapsi*, and *C. trichiurisi* by the more anterior position of the nerve ring. These 5 worms are all very similar and appear to be distinguished only by minor differences of interpretation; they may be regarded as synonymous, with *C. chauhani* receiving priority. This material may be distinguished from *C. longimonospicula* by the number of preanal (7 vs. 6) and postanal (4 vs. 7) papillae.

4.3.3. ***Spirocamallanus istiblenni*** Noble, 1966 Fig. 4-3

General

Nematoda, Spirurida, Camallanoidea, Camallanidae, Procamallaninae, *Spirocamallanus*. Translucent red in life. Long slender worms. Anterior portion of buccal capsule thin and transparent in *en face* view with lateral cords running to anterior margin of capsule. Oral opening oval to rectangular. Cephalic papillae arranged in 3 concentric rings of 4 each. Amphids lateral, at level of middle ring of cephalic papillae. Amphidial pouches conspicuous. Median teeth (see Petter and Thatcher, 1988) not seen. Lateral hypodermal cords prominent, running length of worm, rugose. Buccal capsule supported by 8 cuticular reinforcements to which cephalic muscles attach. Buccal capsule elongate, generally longer than wide, greatest width at two thirds length from anterior margin, lined with spiral ridges (some discontinuous), with basal ring. Two cervical papillae (anterior deirids) present, lateral, usually two thirds of distance from posterior margin of buccal capsule to nerve ring. Esophagus long and slender; divided into anterior claviform muscular portion and posterior glandular portion. Glandular esophagus projecting slightly into intestine in valve-like formation. Excretory pore near level of junction between muscular and glandular esophagus. Phasmids present. Tail of both sexes terminating with two spine-like projections (mucrons), one dorsal and one ventral, occasionally abraded.

Male (4 specimens)

Length 15,683 ± 1,335 (14,275-17,491), maximum width near midbody 258 ± 17 (233-271). Buccal capsule 89 ± 5 (83-94) long, including ring at base 7 ± 2 (5-9) long, 71 ± 1 (70-72) at widest point, length/width ratio 1.25 ± 0.05 (1.18-1.31). Buccal capsule with 13 ± 2 (12-15) spirals when counted diagonally, upper fifth smooth. Muscular esophagus 372 ± 16 (349-384) long, glandular esophagus 593 ± 51 (549-658) long, ratio 1.59 ± 0.1 (1.48-1.73). Cervical papillae 190 ± 22 (173-222) from apex. Nerve ring 244 ± 10 (230-252) from apex. Excretory pore 518 ± 35 (477-564) from apex. Anterior flexure of testis 2,324 ± 664 (1,460-3,072) from apex. Alae well developed, extend 476 ± 13 (463-491) from posterior extremity, posterior end of alae united ventrally 61 ± 3 (57-64) from posterior extremity. Caudal papillae 10; 3 preanal pedunculate papillae, 2 adanal pedunculate papillae not attached to alae, 5 postanal pedunculate papillae. Second preanal papilla 65 % ± 4 (60-70) of distance from first to third papillae. First 2 postanal papillae grouped and separated from next 3 which are generally evenly spaced. Phasmids lateral, slightly posterior to union of alae, 47 ± 3 (43-50) from posterior extremity. Spicules two, unequal, similar in shape, taper to fine point; left spicule (3 specimens) 198 ± 22 (185-223), right spicule (3 specimens) 281 ± 20 (263-302), ratio 1.42 ± 0.07 (1.35-1.50). Gubernaculum absent. Anus 171 ± 10 (158-181) from posterior extremity. Tail flexed ventrally, with prominent lateral muscle bands, gradually tapers to a point. Terminal spines 3 ± 0 (3-4) long.

Female (1 specimen)

Length 17,110, maximum width near midbody 311. Buccal capsule 101 long, including ring at base 5 long, 76 at widest point, length/width ratio 1.32. Buccal capsule with 15 spirals when counted diagonally, upper fifth smooth. Muscular esophagus 421 long, glandular esophagus 687 long, ratio 1.63. Cervical papillae 193 from apex. Nerve ring 275 from apex. Excretory pore 554 from apex. Anterior flexure of ovary 2,205 from apex. Vulva 7,435 or 43 % of body length from apex. Vagina directed posteriorly from vulva, fusiform, muscular, vagina vera tapers gradually into vagina uterina, vagina vera 356 long, 81 at greatest width, vagina uterina 1,595 long, 25 wide. Uterus amphidelphic, posterior ovary reduced. Larvae present within voluminous uterus, occupying most of body cavity and obscuring ovary. Anus 167 from base of terminal digit, anal muscles prominent. Phasmids lateral, approximately half way between anus and base of terminal digit, 59 from base of terminal digit. Tail rounded, with digit-like projection 48 long. Terminal spines 4 long.

Host: *Istiblennius zebra* (Vaillant and Sauvage, 1875) (Perciformes, Blennidae).

Locality: tide pools on Kaupo Beach near Waimanalo, O'ahu, Hawai'i, U.S.A.

Date of collection: January, 1996.

Site in host: intestines.

Prevalence: 17 % (2/12)

Mean intensity: 2.0

Other localities and hosts: 1) Hawai'i from *Entomacrodus marmoratus* (Perciformes, Blennidae) (9 infected of 10 examined; 3.5 mean intensity) and *Eleotris sandwicensis* (Eleotridae) (9/10; 4.6); 2) Fiji from *Bothus pantherinus* (Pleuronectiformes, Bothidae) (3.5; 1.7); and 3) Moorea in French Polynesia from *Zebrasoma scopas* (Perciformes, Acanthuridae) (1/18; 2), *Lutjanus kasmira* (Lutjanidae), *Mulloides flavolineatus* (Mullidae) (2/2; 2.0), *Bothus mancus* (1/1; 5), and *B. pantherinus* (Pleuronectiformes, Bothidae) (4/4; 7.5).

Specimens deposited: 1) Hawai'i, 1 male and 1 female each from *Istiblennius zebra* (USNPC 86742), *Entomacrodus marmoratus* (Muséum National D'Histoire Naturelle of France (MNHN) 505 HF, USNPC 86743), *Eleotris sandwicensis* (MNHN 506 HF, USNPC 86744); 2) Fiji, 1 male and 1 female from *Bothus pantherinus* (USNPC 86747); and 3) Moorea in French Polynesia, 1 male and 1 female each from *Lutjanus kasmira* (MNHN 509 HF, USNPC 86748), *Mulloides flavolineatus* (MNHN 507 HF, USNPC 86745), and *B. pantherinus* (MNHN 508 HF, USNPC 86746).

Previously reported: 1) Hawai'i from *Istiblennius zebra* (Perciformes, Blennidae) (see Noble 1966) and 2) Okinawa, Japan from *Valencienna strigata* (Perciformes, Gobiidae), *Plectorhynchus picus*, *Scolopsis bilineatus* (Haemulidae), *Parapercis cylindrica*, *P. polyphthalma* (Pinguipedidae), *Amphiprion clarkii* (Pomacentridae), *Variola albimarginata*, *V. louti* (Serranidae), *Bothus pantherinus* (Pleuronectiformes, Bothidae), and *Soleichthys heterorhinos* (Soleidae) (see Hasegawa et al. 1991) (some of this material may represent another species and these records should be reevaluated).

Remarks

Worms similar to those found in *Istiblennius zebra* were also found in tide pool specimens of *Entomacrodus marmoratus* (Blennidae), brackish pond and stream mouth specimens of *Eleotris sandwicensis* (Eleotridae) (but not in freshwater specimens sampled from the same island) from Hawai'i, and in the coral reef associated fishes listed above from Fiji and Moorea. These worms agreed with my specimens from *I. zebra* in the number and relative positions of the caudal papillae, shape of the buccal capsule, relative number of buccal capsule spirals, relative positions of the deirid, nerve ring, excretory pore, and vulva, ratio between the two portions of the esophagus, shape of the female tail, presence of a terminal digit in the female, two tail spines in both sexes, and spicule ratio (Table 4-2). Despite differing fixation methods among island localities, measurements of the specimens overlapped strongly (Table 4-2) and fixation method was therefore not considered to have a significant affect on morphology. Based on these similarities, I believe these worms to be conspecific with those recovered from *Istiblennius zebra* and I regard the differences among the worms as individual or host induced variation.

The presence of a sclerotized buccal capsule with spiral linings and without lips places these worms in the genus *Spirocamallanus*. Twenty five spirocamallanid species have been reported from the Indo-Pacific, 4 species of which have been reported from the Pacific with two unequal spicules (Andrade-Salas et al. 1994): *Spirocamallanus guttatusi* (Machida and Taki, 1985), *S. istiblenni* Noble, 1966, *S. monotaxis* Olsen, 1952, and *S. philippinensis* Velasquez, 1980. The present worms agree with Noble's (1966) measurements of *S. istiblenni* (Table 4-2), including my measurements of the relative distances among the preanal papillae in Noble's syntypes. Though Noble reported six postanal papillae in *S. istiblenni*, five postanal papillae and a phasmid (as in my material) were figured and were observed in the syntypes. Also, while the third through fifth postanal papillae were figured as being close together by Noble (1966), examination of the syntypes revealed that they were generally further apart and agreed more closely with my specimens. Additionally, from the present material, one of the males examined agreed with the others for all characters examined except that it lacked spicules. Measurements from this individual have been included with the others as it merely appears to be a mutant lacking spicules. Therefore, I assign this material to *Spirocamallanus istiblenni* Noble, 1966.

The present material may be distinguished from *Spirocamallanus guttatusi* by the shorter length of the alae (463-491 vs. 610-720), spicules (left spicule: 185-223 vs. 200-260; right spicule: 263-302 vs. 300-350), and the longer vagina vera (356 vs. 100-150) for worms of approximately the same size. The inner ring of cephalic papillae of *S. guttatusi* do not appear to have been figured; however, those cephalic papillae that are figured are in agreement with my material. This material may also be distinguished from *S. monotaxis* by the arrangement of the preanal caudal papillae (the second preanal papilla, in my material, was 60-70 % of the distance from the first to the third preanal papilla vs. 35-48 % in *S. monotaxis*). This material, and other similar worms (e.g., *S. guttatusi* and *S. monotaxis*), cannot be reliably differentiated from the description of *S. philippinensis* except by the anteriorly directed vagina in *S. philippinensis*, which appears to be an artifact of fixation. As type specimens were not deposited in the USNPC, as stated in the description (J. R. Lichtenfels, personal communication), *S. philippinensis* should be regarded as *inquirenda*.

Hasegawa et al. (1991) reported *S. istiblenni* from several species of coral reef associated fishes in Okinawa, Japan. In my examination of some of that material (see above), the females examined lacked spine-like projections (mucrons) on the terminal digit and the distribution of the preanal caudal papillae was not consistent with my concept of this species (the second preanal papilla was 44-60 % of the distance from the first to the third preanal papillae). These differences suggest that more than one species may be included in their material. Therefore, the material from Okinawa needs to be reexamined. In the meantime, I have not included their published measurements in this paper.

These records significantly increase the geographic range of *S. istiblenni* to include widely spaced islands in the tropical Pacific Ocean. As this species appears to have a very low host specificity (currently recorded from 8 species from 6 families), and fishes of these families are widespread throughout the Indo-Pacific (e.g., see Myers 1992), it would seem likely that suitable hosts may be found on islands throughout the Indo-Pacific, and that further investigation of the helminth parasites of coral reef fishes in the Indo-Pacific may reveal a much greater geographic range of these worms. While the type locality of this worm is Hawai'i, it must be noted that 8 years prior to its description, several thousand *Lutjanus kasmira*, one of the hosts of this worm (see above) and other related fishes that may have been potential hosts, were taken from French Polynesia and released in Hawai'i (Randall 1987). Thus, the order in which Hawai'i and French Polynesia were colonized by these worms, and by what means, is unknown.

4.3.4. *Spirocamallanus monotaxis* Olsen, 1952 Fig. 4-4

General

Nematoda, Spirurida, Camallanoidea, Camallanidae, Procamallaninae, *Spirocamallanus*. Translucent red in life. Long slender worms. Anterior portion of buccal capsule thin and transparent in *en face* with lateral cords running to anterior margin of capsule. Oral opening oval to square. Cephalic papillae arranged in 3 concentric rings of 4 each. Amphids lateral, at level of middle ring of cephalic papillae. Amphidial pouches conspicuous. Median teeth (see Petter and Thatcher, 1988) absent. Lateral hypodermal cords prominent, running length of worm, rugose. Buccal capsule supported by 8 cuticular reinforcements to which cephalic muscles attach. Buccal capsule elongate, generally longer than wide, greatest width at two thirds length from anterior margin, lined with spiral ridges (some discontinuous), with basal ring. Two cervical papillae (anterior deirids) present, lateral, usually two thirds of distance from posterior margin of buccal capsule to nerve ring. Esophagus long and slender; divided into anterior claviform muscular portion and posterior glandular portion. Glandular esophagus projecting slightly into intestine in valve-like formation. Excretory pore near level of junction between muscular and glandular esophagus. Phasmids present. Tail of both sexes terminating with two spine-like projections (mucrons), one dorsal and one ventral, occasionally abraded.

Male (6 specimens)

Length 21,786 ± 2,170 (18,656-24,948), maximum width near midbody 318 ± 52 (217-354). Buccal capsule 78 ± 7 (69-89) long, including ring at base 8 ± 2 (6-11) long, 60 ± 2 (56-62) at widest point, length/width ratio 1.29 ± 0.09 (1.18-1.45). Buccal capsule with 11 ± 2 (10-14) spiral ridges when counted diagonally, upper fifth smooth. Muscular esophagus 482 ± 31 (443-515) long, glandular esophagus 828 ± 98 (698-982) long, ratio 1.71 ± 0.11 (1.58-1.91). Cervical papillae 192 ± 15 (172-207) from apex. Nerve ring 308 ± 19 (279-334) from apex. Excretory pore 639 ± 69 (572-713) from apex. Anterior flexure of testis 3,552 ± 529 (2,814-4,323) from apex. Alae well developed, extend 726 ± 71 (637-846) from posterior extremity, posterior end of alae united ventrally 60 ± 20 (25-

78) from posterior extremity. Caudal papillae 10; 3 preanal pedunculate papillae, 2 adanal pedunculate papillae not attached to alae, 4 postanal pedunculate papillae. Second preanal papilla 44 % ± 4 (35-48) of distance from first to third papillae, usually appearing closer to first than third papilla, first 2 postanal papillae evenly spaced, next 2 usually grouped. Phasmids lateral, 51 ± 10 (42-68) from posterior extremity. Spicules 2, unequal, similar in shape, taper to fine point; left spicule 189 ± 8 (181-204), right spicule 261 ± 26 (226-292), ratio 1.38 ± 0.13 (1.22-1.53). Gubernaculum absent. Anus 201 ± 16 (184-224) from posterior extremity. Tail flexed ventrally, with prominent lateral muscle bands, gradually tapers to a point. Terminal spines 4 ± 2 (0-6) long.

Female (10 specimens)

Length 27,335 ± 6,659 (11,540-34,096), maximum width near midbody 545 ± 117 (286-674). Buccal capsule 83 ± 5 (72-91) long, including ring at base 10 ± 3 (7-16) long, 75 ± 4 (69-80) at widest point, length/width ratio 1.11 ± 0.07 (0.99-1.24). Buccal capsule with 9 ± 1 (8-10) spiral ridges when counted diagonally, upper fifth smooth. Muscular esophagus 526 ± 55 (455-601) long, glandular esophagus 830 ± 121 (587-996) long, ratio 1.57 ± 0.13 (1.29-1.77). Cervical papillae 197 ± 27 (147-245) from apex. Nerve ring 303 ± 40 (233-350) from apex. Excretory pore 649 ± 142 (414-835) from apex. Anterior flexure of ovary 2,036 ± 292 (1,454-2,403) from apex. Vulva 12,444 ± 2,963 (5,502-15,263) or 46 % ± 2 (41-49) of body length from apex. Vagina directed posteriorly from vulva, fusiform, muscular, vagina vera tapers gradually into vagina uterina, vagina vera 644 ± 119 (438-820) long, 87 ± 14 (62-105) at greatest width, vagina uterina 1,977 ± 556 (634-2,596) long, 26 ± 5 (17-31) wide. Uterus amphidelphic, posterior ovary reduced. Larvae present within voluminous uterus, occupying most of body cavity, obscuring ovary. Anus 167 ± 50 (87-241) from base of terminal digit, anal muscles prominent. Phasmids lateral, approximately half way between anus and base of terminal digit, 78 ± 15 (55-103) from base of terminal digit. Tail rounded, with digit-like projection 34 ± 4 (30-43) long. Terminal spines 4 ± 2 (0-5) long.

Host: *Monotaxis grandoculis* Forsskål, 1775 (Perciformes, Lethrinidae).

Locality: barrier reef of Moorea, Society Islands, and lagoon of Rangiroa, Tuamotu Islands, French Polynesia.

Date of Collection: May, 1995.

Site in host: intestines.

Prevalence: 80 % (4/5)

Mean intensity: 5.5 ± 3 (3-9)

Other Hosts: *Gymnothorax gracilicaudus* (Anguilliformes, Muraenidae) (Moorea; 1 infected of 1 examined, intensity 3), *Saurida gracilis* (Aulopiformes, Synodontidae) (Moorea; 1/2, 4), *Neoniphon opercularis* (Beryciformes, Holocentridae) (Moorea; 1/1, 1),*Valencienna strigatus* (Perciformes, Gobiidae) (Rangiroa; 1/1, 6), *Cheilinus chlorourus* (Moorea; 3/4, 2.0), *Thalassoma hardwicke* (Labridae) (Moorea; 2/4, 2.5), *Gnathodentex aureolineatus* (Moorea; 3/3, 6.7), *Lethrinus olivaceus* (Lethrinidae) (Rangiroa; 1/4, 1), *Parapercis millipunctata* (Pinguipedidae) (Moorea; 1/1, 3), and *Epinephelus merra* (Serranidae) (Moorea, Tahiti, and Tetiaroa: 15/104, 3.0).

Specimens deposited: USNPC XXXXX and French National Museum of Natural History XXXX.

Previously reported: Hawai'i from *Monotaxis grandoculis* (Percifomes, Lethrinidae) (see Olsen, 1952).

Remarks

Worms similar to those found in *Monotaxis grandoculis* were found in the coral reef associated fishes listed above. These worms agreed with my specimens from *Monotaxis grandoculis* in the number and relative positions of the caudal and cephalic papillae, shape of the buccal capsule, number of spiral ridges of the buccal capsule, relative positions of the deirid, nerve ring, excretory pore, and vulva, ratio between the two portions of the esophagus, shape of the female tail, presence of a terminal digit in the female, two tail spines in both sexes, and spicule ratio (Table 4-3). Based on the above similarities, I believe these worms to be conspecific with the worms recovered from *Monotaxis grandoculis* and regard the differences among the worms as individual or host induced variation.

The presence of a sclerotized buccal capsule with spiral linings places these worms in the genus *Spirocamallanus*. Twenty four species of *Spirocamallanus* have been reported from the Indo-Pacific, but only 3 of these have been reported from the Pacific with 2 unequal spicules (Andrade-Salas et al. 1994): *Spirocamallanus guttatusi* (Machida and Taki, 1985), *S. istiblenni* Noble, 1966, and *S. monotaxis* Olsen, 1952. The present material agrees with the type specimens of *S. monotaxis* in number and disposition of caudal papillae, position of the excretory pore, and Olsen's (1952) measurements except the number of spiral ridges in the male buccal capsule and the length of the buccal capsule (Table 4-3). Considering the range of variation in the number of spiral ridges lining the buccal capsule observed in the present material, the deviation in the number of spiral ridges lining the buccal capsule between the present material and *S. monotaxis* does not appear great enough to be considered diagnostic. Based on the considerable range of variation in my material, the greater length of the buccal capsule in the type specimens does not appear to be diagnostic, especially considering the small number of specimens examined. Therefore, I assign this material to *Spirocamallanus monotaxis* Olsen, 1952.

The present worms may be distinguished from *Spirocamallanus guttatusi* by the shorter right spicule (226-292 vs. 307 and 311 in the 2 *S. guttatusi* examined), the lower spicule ratio (1.22-1.53 vs. 1.66 and 1.68 in the 2 *S. guttatusi* examined), the distance of the first to second preanal papilla relative to the distance of the first to third preanal papilla (35-48 % vs. 71 % [figured]), and the number of cephalic papillae. The inner ring of cephalic papillae of *S. guttatusi* do not appear to have been figured; however, the cephalic papillae figured are in agreement with my material. The present worms may be distinguished from *S. istiblenni* by the distance of the first to second preanal papilla relative to the distance of the first to third preanal papilla (35-48 % vs. 60-75 %).

4.3.5. ***Spirocamallanus colei*** n. sp. Fig. 4-5

General

Nematoda, Spirurida, Camallanoidea, Camallanidae, Procamallaninae, *Spirocamallanus*. Translucent red in life. Long slender worms. Anterior portion of buccal capsule thin and transparent in *en face* with lateral cords running to anterior margin of capsule. Oral opening oval to square. Cephalic papillae arranged in 3 concentric rings of 4 each. Amphids lateral, at level of middle ring of cephalic papillae. Amphidial pouches not seen. Median teeth (see Petter and Thatcher, 1988) absent. Lateral hypodermal cords prominent, running length of worm, rugose. Buccal capsule supported by 8 cuticular reinforcements to which cephalic muscles attach. Buccal capsule elongate, longer than wide, greatest width at two thirds length from anterior margin, lined with spiral ridges (some discontinuous), with basal ring. Cervical papillae (anterior deirids), present, lateral, usually two thirds of distance from posterior margin of buccal capsule to nerve ring. Esophagus long and slender; divided into anterior claviform muscular portion and posterior glandular portion. Glandular esophagus projecting slightly into intestine in valve-like formation. Excretory pore near level of junction between muscular and glandular esophagus. Phasmids present. Tail of both sexes simple, tapering to a point, without spine-like projections (mucrons).

Male (4 specimens)

Length 13,571 ± 3,727 (10,098-17,571), maximum width near midbody 212 ± 77 (146-296). Buccal capsule 92 ± 17 (76-113) long, including ring at base 8 ± 3 (6-12) long, 62 ± 7 (55-71) at widest point, length/width ratio 1.48 ± 0.18 (1.33-1.74). Buccal capsule with 16 ± 2 (14-18) spiral ridges when counted diagonally, upper fifth smooth. Muscular esophagus 274 ± 80 (192-361) long, glandular esophagus 377 ± 89 (267-459) long, ratio 1.40 ± 0.14 (1.22-1.55). Cervical papillae 173 ± 36 (133-216) from apex. Nerve ring 212 ± 43 (172-255) from apex. Excretory pore 400 ± 146 (257-528) from apex. Anterior flexure of testis 3,314 ± 853 (2,690-4,566) from apex. Alae well developed, extend 468 ± 111(329-578) from posterior extremity, posterior end of alae united ventrally 47 ± 18

(31-73) from posterior extremity. Caudal papillae 10; 3 preanal pedunculate papillae, 2 adanal pedunculate papillae not attached to alae, 5 postanal pedunculate papillae. Second preanal papilla 61 % ± 4 (57-65) of distance from first to third papillae, postanal papillae generally evenly spaced. Phasmids lateral, slightly posterior to union of alae, 18 ± 3 (14-22) from posterior extremity. Spicules 2, unequal, similar in shape, taper to fine point; left spicule 208 ± 25 (177-231), right spicule 338 ± 44 (292-377), ratio 1.62 ± 0.06 (1.54-1.68). Gubernaculum absent. Anus 160 ± 51 (105-205) from posterior extremity. Tail flexed ventrally with prominent lateral muscle bands.

Female (13 specimens)
Length 29,463 ± 4,926 (21,121-36,195), maximum width near midbody 407 ± 64 (300-520). Buccal capsule 100 ± 8 (88-110) long, including ring at base 7 ± 2 (5-12) long, 76 ± 6 (67-87) at widest point, length/width ratio 1.32 ± 0.08 (1.14-1.47). Buccal capsule with 15 ± 2 (12-18) spiral ridges when counted diagonally, upper fifth smooth. Muscular esophagus 365 ± 48 (280-431) long, glandular esophagus 478 ± 67 (363-579) long, ratio 1.33 ± 0.23 (1.04-1.85). Cervical papillae 217 ± 27 (174-270) from apex. Nerve ring 256 ± 22 (207-280) from apex. Excretory pore (12 specimens) 488 ± 79 (386-624) from apex. Anterior flexure of ovary 3,164 ± 875 (2,154-5,143) from apex. Vulva 12,128 ± 2,037 (8,435-14,498) or 41 % ± 3 (35-45) of body length from apex. Vagina directed posteriorly from vulva, fusiform, muscular, vagina vera tapers gradually into vagina uterina, vagina vera 377 ± 59 (264-469) long, 72 ± 17 (38-96) at greatest width, vagina uterina (10 specimens) 1,732 ± 544 (972-2,665) long, 40 ± 16 (21-76) wide. Uterus amphidelphic, posterior ovary reduced. Larvae present within voluminous uterus, occupying most of body cavity, obscuring ovary. Anus 262 ± 54 (188-346) from posterior extremity, anal muscles prominent. Phasmids lateral, more prominent in dorso-ventral view, 134 ± 24 (106-180) from posterior extremity.

Type host: *Acanthurus achilles* Shaw, 1803 (Perciformes, Acanthuridae).
Type locality: outer slope of Rangiroa, Tuamotu Islands, French Polynesia.
Date of Collection: May, 1995.

Site in host: intestines.

Prevalence: 100 % (2/2).

Mean intensity: 3.0 (2-4).

Other hosts: *Acanthurus guttatus* (Moorea; 1/1, 2), *Acanthurus lineatus* (Moorea; 1/2, 3), *Acanthurus triostegus* (Moorea and Rangiroa; 6/8, 1.5), and *Zebrasoma scopas* (Perciformes, Acanthuridae) (Moorea; 2/24, 1.0).

Specimens deposited: USNPC XXXXX and French National Museum of Natural History XXXX.

Remarks

Worms similar to those found in *Acanthurus achilles* were found in the coral reef associated fishes listed above. These worms agreed with my specimens from *Acanthurus achilles* in the number and relative positions of the caudal and cephalic papillae, shape of the buccal capsule, number of spiral ridges of the buccal capsule, relative positions of the deirid, nerve ring, excretory pore, and vulva, ratio between the two portions of the esophagus, shape of the female tail, absence of tail spines in both sexes, and spicule ratio. Based on the above similarities, I believe these worms to be conspecific with the worms recovered from *Acanthurus achilles* and have included measurements of worms from the other hosts with those of worms from *Acanthurus achilles* to offset small sample size and give a better range of variation.

The presence of a sclerotized buccal capsule with spiral linings and without lips places these worms in the genus *Spirocamallanus*. The only *Spirocamallanus* from the Indo-Pacific which has unequal spicules and a tapered tail in the female is *S. otolithi* Gupta and Garg, 1986 (see Andrade-Salas et al. 1995). The present worms may be distinguished from *S. otolithi* by the position of the nerve ring (172-255 vs. 717 from apex in the one male *S. otolithi* reported), the much shorter lengths of the muscular and glandular esophagi (192-361 and 267-459, respectively, vs. 1,000 and 1,266, respectively, in males; 280-431 and 363-579, respectively, vs. 700-820 and 933-1,112, respectively, in females), the number of postanal papillae (5 vs. 3), and the lower spicule ratio (1.54-1.68 vs. 2.3).

The number of postanal papillae in *S. otolithi* may be greater than stated in the description as postanal papillae are difficult to detect in lateral view given in the description (lateral). I therefore designate this material a new species, *Spirocamallanus colei* Rigby and Adamson, 199X.

Etymology: This species is named after Brandon Cole, a good friend.

4.3.6. ***Spirocamallanus chaimha*** n. sp. Fig. 4-6

General

Nematoda, Spirurida, Camallanoidea, Camallanidae, Procamallaninae, *Spirocamallanus*. Translucent red in life. Long slender worms. Anterior portion of buccal capsule thin and transparent in *en face* with lateral cords running to anterior margin of capsule. Oral opening oval to square. Cephalic papillae arranged in 3 concentric rings of 4 each. Amphids lateral, at level of middle ring of cephalic papillae. Amphidial pouches not seen. Median teeth (see Petter and Thatcher, 1988) absent. Lateral hypodermal cords prominent, running length of worm, rugose. Buccal capsule supported by 8 cuticular reinforcements to which cephalic muscles attach. Buccal capsule elongate, longer than wide, greatest width at two thirds length from anterior margin, lined with spiral ridges (some discontinuous), with basal ring. Cervical papillae (anterior deirids) absent. Esophagus long and slender; divided into anterior claviform muscular portion and posterior glandular portion. Glandular esophagus projecting slightly into intestine in valve-like formation. Excretory pore near level of junction between muscular and glandular esophagus. Phasmids present. Tail of both sexes simple, without spine-like projections (mucrons).

Male (3 specimens)

Length 13,210 ± 1,867 (11,119-14,707), maximum width near midbody 216 ± 32 (185-248). Buccal capsule 93 ± 8 (86-102) long, including ring at base 8 ± 1 (8-9) long, 66 ± 2 (64-68) at widest point, length/width ratio 1.40 ± 0.10 (1.30-1.49). Buccal capsule with

25 ± 2 (23-27) spiral ridges when counted diagonally, upper fifth smooth. Muscular esophagus 302 ± 17 (285-318) long, glandular esophagus 461 ± 21 (440-482) long, ratio 1.52 ± 0.02 (1.51-1.54). Nerve ring 192 ± 17 (175-209) from apex. Excretory pore 408 ± 51 (374-467) from apex. Anterior flexure of testis 4,150 ± 1,565 (2,392-5,391) from apex. Alae well developed, extend 520 ± 28 (488-537) from posterior extremity, posterior end of alae united ventrally 53 ± 9 (44-62) from posterior extremity. Caudal papillae 10; 3 preanal pedunculate papillae, 2 adanal pedunculate papillae not attached to alae, 5 postanal pedunculate papillae. Second preanal papilla 62 % ± 3 (59-65) of distance from first to third papillae, first 2 postanal papillae evenly spaced, next 2 generally grouped, fifth postanal papilla midway between fourth postanal papilla and phasmid. Phasmids lateral, slightly posterior to union of alae, 22 ± 3 (19-25) from posterior extremity. Spicules 2, unequal, similar in shape, taper to fine point; left spicule 182 ± 17 (170-202), right spicule 262 ± 24 (244-289), ratio 1.44 ± 0.05 (1.40-1.49). Gubernaculum absent. Anus 155 ± 20 (140-178) from posterior extremity. Tail flexed ventrally, with prominent lateral muscle bands, gradually tapers to a point.

Female (4 specimens)

Length 18,311 ± 3,472 (14,987-23,153), maximum width near midbody 335 ± 59 (285-416). Buccal capsule 107 ± 5 (102-114) long, including ring at base 10 ± 2 (7-11) long, 79 ± 4 (74-82) at widest point, length/width ratio 1.36 ± 0.09 (1.29-1.47). Buccal capsule with 25 ± 1 (23-26) spiral ridges when counted diagonally, upper fifth smooth. Muscular esophagus 323 ± 14 (308-342) long, glandular esophagus 479 ± 27 (455-509) long, ratio 1.48 ± 0.07 (1.42-1.58). Nerve ring 203 ± 18 (185-222) from apex. Excretory pore 425 ± 43 (374-477) from apex. Anterior flexure of ovary 1,602 ± 850 (733-2,345) from apex. Vulva 8,317 ± 1,498 (6,883-10,307) or 45 % ± 2 (44-47) of body length from apex. Cuticle surrounding vulva rugose and raised. Vagina directed posteriorly from vulva, fusiform, muscular, vagina vera tapers gradually into vagina uterina, vagina vera 218 ± 23 (191-237) long, 58 ± 7 (48-64) at greatest width, vagina uterina (2 specimens) 801 and 1,214 long, 26 and 38 wide. Uterus amphidelphic, posterior ovary reduced. Larvae present within voluminous uterus, occupying most of body cavity, obscuring ovary. Anus

217 ± 24 (200-253) from posterior extremity, anal muscles prominent. Phasmids obscure, visible only in ventral view, lateral, 114 ± 19 (92-140) from posterior extremity. Tail rounded, terminal digit-like projection absent.

Type host: *Ctenochaetus striatus* (Quoy and Gaimard, 1825) (Perciformes, Acanthuridae).
Type locality: barrier reef of Moorea, Society Islands, French Polynesia.
Date of Collection: May, 1995.
Site in host: intestines.
Prevalence: 67 % (4/6).
Mean intensity: 2 ± 1.41 (1-4).
Other hosts: *Acanthurus olivaceus* (Perciformes, Acanthuridae) (Moorea; 1/1, 1).
Specimens deposited: USNPC XXXXX and French National Museum of Natural History XXXX.

Remarks

A female worm similar to those found in *Ctenochaetus striatus* was found in the coral reef associated fish *Acanthurus olivaceus*. This worm agreed with my specimens from *Ctenochaetus striatus* in the shape of the buccal capsule, number of spiral ridges of the buccal capsule, absence of the deirid, relative positions of the nerve ring, excretory pore, and vulva, ratio between the two portions of the esophagus, shape of the female tail, absence of a terminal digit in the female, and the absence of tail spines. Based on the above similarities, I believe this worm to be conspecific with the worms recovered from *Ctenochaetus striatus* and have included its measurements with those of worms from *Ctenochaetus striatus* to offset small sample size and give a better range of variation.

The presence of a sclerotized buccal capsule with spiral linings places these worms in the genus *Spirocamallanus*. This material is distinguished from all of the 24 species of *Spirocamallanus* reported from the Indo-Pacific with unequal spicules (Andrade-Salas et al., 1995) by a rugose cuticular projection associated with the vulva and a rounded female tail lacking a terminal digit. I therefore designate this material a new species, *Spirocamallanus chaimha* Rigby and Adamson, 199X.

The present worms may be distinguished from the 5 previously described *Spirocamallanus* reported from the Pacific (*S. colei* n. sp., *S. guttatusi*, *S. istiblenni*, *S. monotaxis*, and *S. platycephali* [see Andrade-Salas et al. 1995]) by the greater number of spiral ridges in the buccal capsule (23-27 vs. 8-20, with 16-20 occurring infrequently, in all other species), the shape of the female tail (rounded without a terminal digit vs. rounded with a terminal digit or tapered), the absence of terminal spine-like projections (present in the other worms, except *S. colei* n. sp.), and the presence of a rugose cuticular projection associated with the vulva (absent in the other worms).

Etymology: The specific name is derived from the Quiché Maya word *chaimha* ("razor house"), referring to the spiral ridges lining the buccal capsule.

4.4. Discussion

Petter (1979*b*) concluded that the number of longitudinal ridges lining the buccal capsule reflects evolutionary affinities in the genus *Camallanus*. However, in some species of *Camallanus* (e.g., see *Camallanus marinus* above), the number of longitudinal ridges lining the buccal capsule varies not only between individuals but also within an individual buccal capsule, being greatest at the anterior margin and decreasing posteriorly. This variation in number of longitudinal ridges means that minor differences are not important but major differences may still of taxonomic significance. Thus, when reporting the number of longitudinal ridges lining the buccal capsule, a measure of the variation observed in the number of longitudinal ridges, and at what position on the buccal capsule they were counted, should be included.

In *Batrachocamallanus* (Camallanidae: Procamallaninae) of African amphibians, Jackson and Tinsley (1995) found that closely related species differ markedly in the structure of buccal capsule ridges; some with longitudinal ridges, spiral ridges, and others lacking ridges. Because of this variation, they concluded that this was an evolutionary unstable characteristic and questioned the presence of buccal capsule ridges as a criterion for generic separation in other procamallanines. However, among the marine *Spirocamallanus* of the Pacific, the presence of spiral ridges appears to be a constant across species lines, although the number of spiral ridges is not constant within a species. Therefore, I suggest that 1) the presence of buccal capsule ridges may be used as a criterion for generic separation among procamallanines other than *Batrachocamallanus* and that 2) the number of spiral ridges lining the buccal capsule of *Spirocamallanus* may be used as a means to distinguish between species if there are major differences in the number of spiral ridges.

Noble (1966) described "buccal sinuses" in the buccal capsules of *Spirocamallanus*. However, these are not sinuses but rather cuticular reinforcements of the buccal capsule, to which the cephalic muscles attach. Such structures are probably present in all members of this genus (and other procamallanines) but may not be visible unless viewed *en face*.

The wide geographic distribution of some of these worms (e.g., *Camallanus marinus*, *Spirocamallanus monotaxis*, and *Spirocamallanus istiblenni* have ranges spanning the tropical southern Pacific) may be achieved through the use of pelagic hosts. Worms of this family have a low specificity for their copepod intermediate hosts (Moravec et al. 1995), permitting them to infect a wide range of copepods, some of which may be pelagic. Camallanid nematodes also appear to be able to infect some pelagic fishes (e.g., *Camallanus marinus* has been reported from epipelagic carangid fishes [Schmidt and Kuntz 1969]), either due to low host specificity or trophic transfer. This potential use of such pelagic hosts for both life history stages may enhance the dispersal ability of these worms.

Petter (1979*a*) proposed that the genus *Spirocamallanus* may be divided into several clades based on the number of preanal papillae and relative sizes of the spicules. One such clade is composed of species of *Spirocamallanus* with 3 preanal papillae and 2 unequal spicules from marine fishes throughout the world. Descriptions of these species would suggest that there is variation in the number of postanal papillae (3-5). However, the last 2 (of 5) papillae are difficult to detect and may only be seen in ventral view. If worms are not examined in ventral view, the last 2 postanal papillae (of 5), and the phasmid, may be overlooked. With further examination, 5 postanal papillae and a phasmid may prove to be an additional characteristic of worms of this clade.

In my examination of species of *Spirocamallanus* from marine fishes of French Polynesia, all 4 species had 3 preanal papillae, 5 postanal papillae, a phasmid, and 2 unequal spicules and, thus, belong to the clade mentioned above. However, the *Spirocamallanus* of French Polynesia may be further divided into 3 groups: worms with a rounded female tail with a terminal digit (*S. istiblenni* and *S. monotaxis*), worms with a rounded female tail, no terminal digit, and a rugose cuticular projection associated with the vulva (*S. chaimha* n. sp.), and worms with a tapered female tail (*S. colei* n. sp.). As the shape of the female tail appears to be constant within a species, this character may reflect more detailed evolutionary affinities within this clade and, therefore, should be examined further.

Spirocamallanus from marine fishes in French Polynesia appeared to exhibit low host specificity (e.g., *S. monotaxis* above was found in 12 fish species of 8 families from 4 orders and *S. istiblenni* has been reported from 8 fish species of 6 families from 2 orders). Although *S. chaimha* n. sp. and *S. colei* n. sp. appear to be limited to acanthurids, I suggest that ecological factors, rather than phylogenetic specificity, are more important determinants of host species range. *Spirocamallanus monotaxis* and *S. istiblenni* were found only in carnivorous fishes while *S. chaimha* n. sp. and *S. colei* n. sp. were found only in herbivorous fishes (with no other herbivorous fishes, such as scarids, examined).

In addition, *S. chaimha* n. sp. appeared to be present only in fishes from protected reefs and *S. colei* n. sp. was found only in fishes of exposed reefs.

Worms with rounded female tails and a terminal digit appear to be widespread throughout the Indo-Pacific and the 2 worms with this female tail morphology reported from French Polynesia (*S. istiblenni* and *S. monotaxis*) have been reported elsewhere. Other worms with tapered female tails, similar to *S. colei* n. sp., have been reported elsewhere in the Indo-Pacific. Therefore, coral reef fishes in French Polynesia appear to have been colonized in at least 3 separate events by worms of this genus: *S. istiblenni*, *S. monotaxis*, and *S. colei* n. sp. *Spirocamallanus chaimha* n. sp., however, differs markedly in female tail morphology, the absence of deirids, and the presence of a raised cuticular projection associated with the vulva; at this point in time, its origin is problematic.

Table 4-1. Comparison of measurements of *Camallanus marinus* from Moorea and the Philippines. Measurements are in µm and are given as ranges. [ ] indicate my measurements from figures in the description and should be viewed with caution.

		Philippines, Schmidt and Kuntz (1969)	Schmidt and Kuntz's material, my measurements	Moorea present study	*C. atropusi* Bashirullah and Khan, 1973	*C. dollfusi* Bashirullah and Khan, 1973	*C. trichiuris* Bashirullah and Rahman, 1972
Host(s)		see text	*Trichiurus haumela*	*Epinephelus merra*	*Atropus atropus*	*Trichiurus haumela*	*Trichiuris savala*
Total length	m	12,000-13,000*		4,952-6,310	11,370-12,530	11,010-11,910	4,980-8,910
	f	15,000-18,000*		6,788-7,548			9,980-12,580
Buccal capsule	m	116-125 x 117-122	100-121 x 92-117	140-152 x 149-159	161-163 x ? [142 x 127]	143 x ? [126 x 117]	
	f	130-147 x 130-150	129-141 x 123-126	162-173 x 162-194			[133 x 136]
Ridges (top, widest, base)	m		45-51,23-26,6-11	50-56,24-27,7-9	[26,25,3]	[38,27,8]	
	f		47-49,23-28,5-9	48-58,24-29,6-9			[29,25,9]
Muscular esophagus	m	1,000-1,100		905-1,170	1,290-1,320	1,196-1,198	720-1,040
	f	1,100-1,200		1,097-1,233			880-1,250
Glandular esophagus	m	1,000-1,200		614-914	1,310-1,320	1,128-1,129	780-1,550
	f	1,200-1,250		996-1,320			1,190-1,330
Ratio M/G esophagi	m	0.92-1.0		1.03-1.47	1.02-1.0	0.94	1.08-1.49
	f	0.92-0.96		0.83-1.22			1.06-1.35
Apex to nerve ring	m		181-205	203-224	217-224 [201]	214-219 [214]	205-231
	f		213-225	208-250			300-340
Apex to excretory pore	m		942-1,280	973	182-189	299-314	
	f		849-1,050	853-1,175			
Alae		360-400		342-427	631-635 [617]	575-581 [646]	493-559 [303]
Number of spicules		1	1	1	1	1	2 [1]
Spicule		275-280		238-248	282-285 [268]	260-263 [216]	231-250 [212]
Pre-, ad-, postanal papillae		7,2,4	7,2,4	7,2,4	7,?,6 [7,2,4]	7,?,4 [7,?,4]	7,?,4 [7,2,4]
Vulva %		50-53		36-53			44-51

Note: *indicates that measurements were originally given in mm (accurate to 1/10 of a mm) and are here presented in µm.

Table 4-2. Comparison of measurements of *Spirocamallanus istiblenni*. Measurements are in µm and given as ranges. [ ] indicate my measurements.

		Noble, 1966	Present study					
Locality		O'ahu	O'ahu	Hawai'i	Hawai'i	Fiji	Moorea	Moorea
Host(s)		*Istiblennius zebra*	*Istiblennius zebra*	*Eleotris sandwicensis*	*Entomacrodus marmoratus*	*Bothus pantherinus*	*Zebrasoma scopas*	*Bothus mancus*
Specimens examined	m	5	4	2	6	1	1	1
	f	9	1	5	6	4	1	
Total length	m	14,900	14,274-17,491	8,334-9,802	8,118-12,255	14,494	19,724	23288
	f	21,500	17,110	10,635-18,834	13,196-19,011	17,475-20,087	27,033	
Buccal capsule	m	75 x 72	83-94 x 70-72	60-61 x 49-53	81-99 x 62-71	76 x 54	67 x 63	77 x 72
	f	77 x 77	101 x 76	67-74 x 58-60	85-101 x 73-79	74-90 x 58-64	70 x 73	
Buccal spirals	m	13-14	12-15	13-15	13-16	11	15	17
	f	13-14	15	11-14	12-16	9-11	12	
Muscular esophagus	m	325	349-384	371-380	323-374	324	418	442
	f	397	421	383-496	387-463	363-419	456	
Glandular esophagus	m	485	549-658	470-479	401-601	535	560	709
	f	588	687	519-723	599-683	451-669	664	
Ratio G/M esophagi	m	1.49	1.48-1.73	1.24-1.29	1.13-1.78	1.65	1.34	1.6
	f	1.48	1.63	1.28-1.55	1.4-1.75	1.24-1.72	1.46	
Deirid	m		173-222	159	174-252	177	171	211
	f		193	156-200	163-208	141-218	170	
Nerve ring	m	208	230-252	214	243-305	214	248	262
	f	220	275	205-255	235-252	231-263	273	
Excretory pore	m	400	477-564	356-452	408-501		536	634
	f	400	554	404-543	497-550	457-506	645	
Alae		[400]	463-491	391-393	407-474	384	496	575
Spicule	l	184	185-223	159-170	171-203	171	168	167
	r	274	263-302	260-266	273-297	225	264	230
Spicule ratio		1.49	1.35-1.5	1.53-1.67	1.4-1.62	1.32	1.57	1.38
Position of 2nd preanal papilla		[74 %]	60-70 %	61-62 %	66-75 %	60 %	67 %	67 %
Vulva %		38 %	43 %	46-51 %	41-44 %	36-48 %	43 %	

Table 4-2. Continued.

Locality Host(s)		Moorea *Bothus pantherinus*	Moorea *Lutjanus kasmira*	Moorea *Mulloides flavolineatus*
Specimens examined	m	6	2	6
	f	10	2	3
Total length	m	9,202-17,523	17,629-17,632	10,386-17,239
	f	14,639-27,902	22,105-24,745	16,975-35,387
Buccal capsule	m	68-86 x 51-78	83-86 x 66-67	64-70 x 60-67
	f	75-91 x 97-96	87-95 x 81-84	74-81 x 79-84
Buccal spirals	m	13-20	16-18	12-16
	f	8-18	11-12	12
Muscular esophagus	m	345-466	378-386	236-402
	f	365-568	469-503	418-505
Glandular esophagus	m	421-724	588-654	367-562
	f	487-772	764-779	442-775
Ratio G/M esophagi	m	1.14-1.57	1.55-1.69	1.18-1.56
	f	1.19-1.46	1.52-1.66	1.06-1.53
Deirid	m	128-205	160-204	124-175
	f	157-226	190-199	168-209
Nerve ring	m	206-277	243-253	194-236
	f	233-318	278-289	254-269
Excretory pore	m	377-556	461-507	452-491
	f	387-721	598-607	410-556
Alae		375-524	544-562	378-536
Spicule	l	151-185	172-177	153-185
	r	246-287	240-263	244-302
Spicule ratio		1.36-1.81	1.39-1.49	1.54-1.78
Position of 2nd preanal papilla		65-72 %	63-69 %	61-71 %
Vulva %		38-44 %	45 %	39-40 %

Table 4-3. Comparison of measurements of *Spirocamallanus monotaxis* from Moorea and Hawaii. Measurements are in µm and given as ranges.

		Olsen (1952)	Olsen's material, my measurements	present study				
Host(s)		*Monotaxis grandoculis*	*Monotaxis grandoculis*	*Monotaxis grandoculis*	*Epinephelus merra*	*Cheilinus chlorourus*	*Lethrinus olivaceus*	*Gymnothorax gracilicaudus*
Locality		Hawaii	Hawaii	Rangiroa and Moorea	Moorea, Tahiti, Tetiaroa	Moorea	Rangiroa	Moorea
specimens	m	2	1	6	11	2	1	3
	f	1	1	10	10	2		
Total length	m	15,800-17,700	16,146	18,656-24,948	7,177-14,286	7,032-10,304	8,255	11,354-13,352
	f	34,000		11,540-34,096	8,914-26,755	9,174-10,683		
Buccal capsule	m	110 x 70	104 x 69	69-89 x 56-62	67-77 x 55-62	66-68 x 56-54	67 x 53	74-76 x 53-61
	f	110 x 80	112 x 72	72-91 x 69-80	72-88 x 65-80	71-72 x 60-64		
Buccal spirals	m	16	16	10-14	10-12	12-13	12	10-14
	f	10	10	8-10	8-11	10-11		
Muscular esophagus	m	390-440	370	443-515	309-384	351-357	404	307-335
	f	590	570	455-601	393-465	403-416		
Glandular esophagus	m	630-760	626	698-982	446-669	429-559	471	488-639
	f	1,110	1,022	587-996	595-905	487-557		
Ratio G/M esophagi	m	1.62-1.73	1.69	1.58-1.91	1.34-1.84	1.2-1.59	1.17	1.59-1.91
	f	1.88	1.79	1.29-1.77	1.28-2.12	1.21-1.34		
Apex to deirid	m		201	172-207	112-182	149-217	170	145-202
	f		262	147-205	159-255	154-162		
Apex to nerve ring	m	280-300	269	279-334	206-249	216-221	223	190-222
	f	370	349	233-350	226-291	238-246		
Apex to excretory pore	m	470	561	572-713	314-568	416-487	446	447
	f		719	414-835	338-759	409-453		
Alae			524	637-846	286-648	352-407	403	366-427
Spicule	r	230-240	182	181-204	132-203	141-157	149	149-171
	l	290-320	244	226-292	190-280	291-260	221	211-257
Spicule ratio		1.26-1.33	1.34	1.22-1.53	1.2-1.87	1.84-1.85	1.49	1.33-157
Pre- and postanal papillae		3,3	3,5	3,5	3,5	3,5	3,5	3,5
Vulva %		40		41-49	27-53	45-48		

Table 4-3. Continued.

Host(s)		*Neoniphon opercularis*	*Saurida gracilis*	*Thalassoma hardwicke*
Locality		Moorea	Moorea	Moorea
specimens	m	1	1	3
	f		3	1
Total length	m	9,337	8,849	4,479-10,957
	f		10,759-13,389	15,889
Buccal capsule	m	75 x 56	71 x 58	60-64 x 47-55
	f		75-80 x 63-67	72 x 65
Buccal spirals	m	13	11	12-13
	f		9-10	10
Muscular esophagus	m	342	337	284-357
	f		382-433	401
Glandular esophagus	m	492	402	316-566
	f		567-589	684
Ratio G/M esophagi	m	1.44	1.19	1.11-1.59
	f		1.36-1.51	1.71
Apex to deirid	m	170	144	134-155
	f		129-154	160
Apex to nerve ring	m	216	210	185-210
	f		225-245	242
Apex to excretory pore	m	464	421	289-523
	f		337-553	534
Alae		388	395	266-420
Spicule	r	170	131	137-182
	l	254	194	201-255
Spicule ratio		1.5	1.48	1.4-1.59
Pre- and postanal papillae		3,5	3,5	3,5
Vulva %			46-47	50

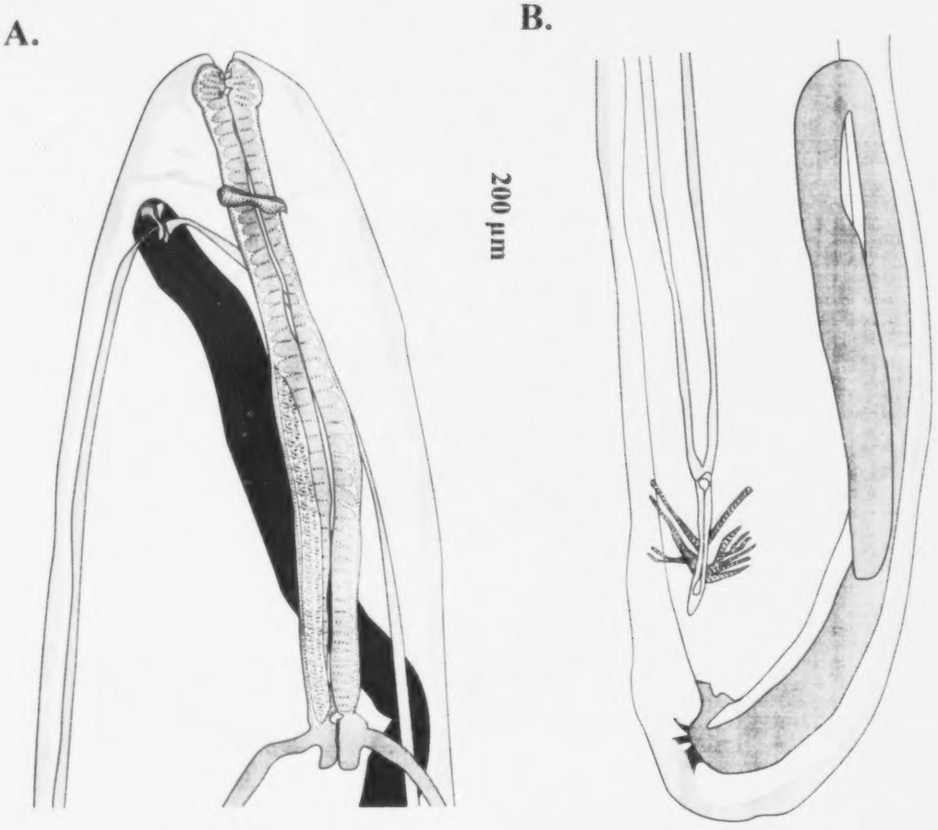

Fig. 4-1. Philometra sp. A. Lateral view of cephalic extremity. B. Lateral view of female caudal extremity.

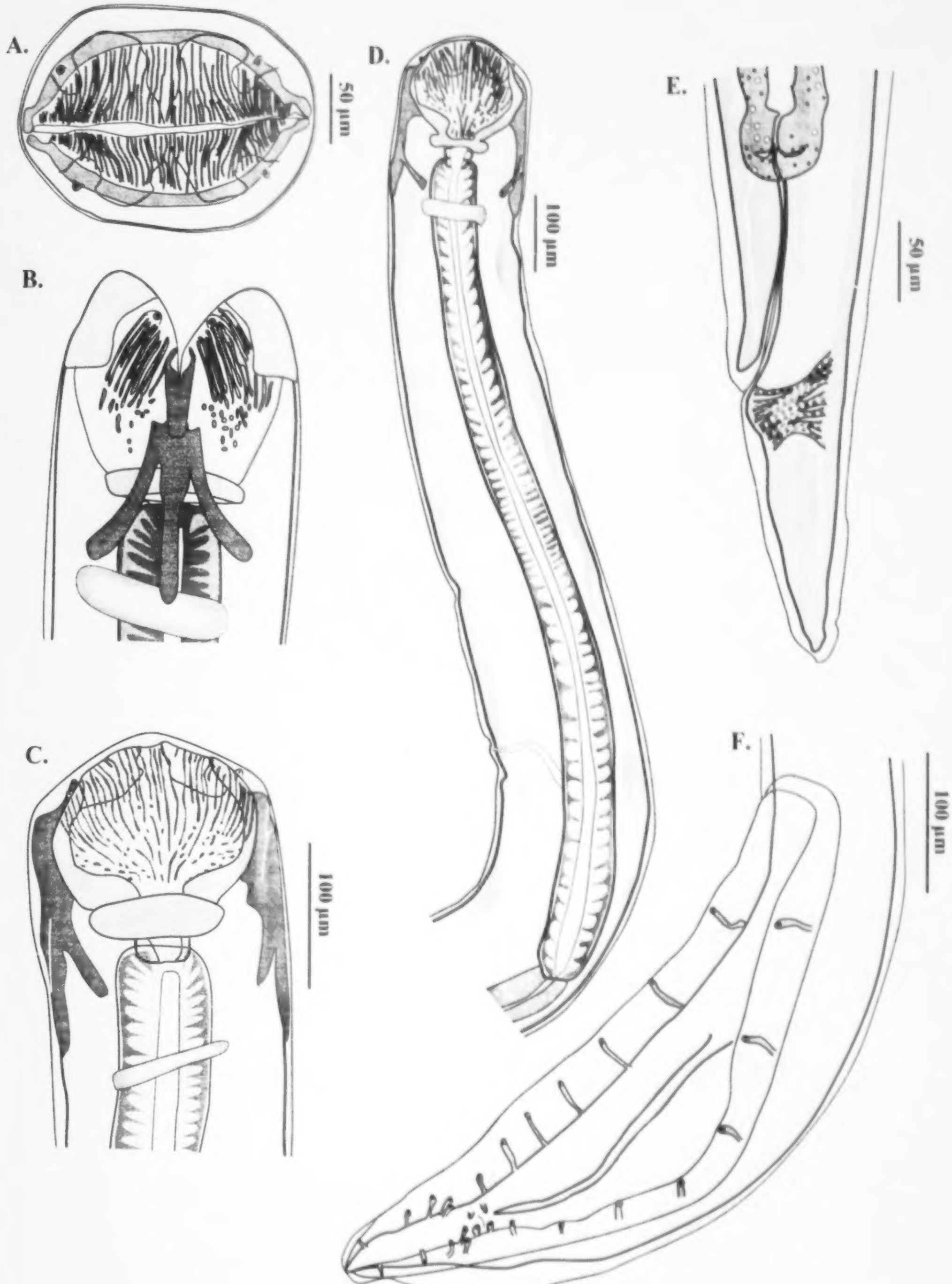
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Fig. 4-2. *Camallanus marinus*. A. En face view of female cephalic extremity. B. Dorso-ventral view of male cephalic extremity. C. Lateral view of male cephalic extremity. D. Lateral view of male esophageal region. E. Lateral view of female caudal extremity. F. Lateral view of male caudal region.

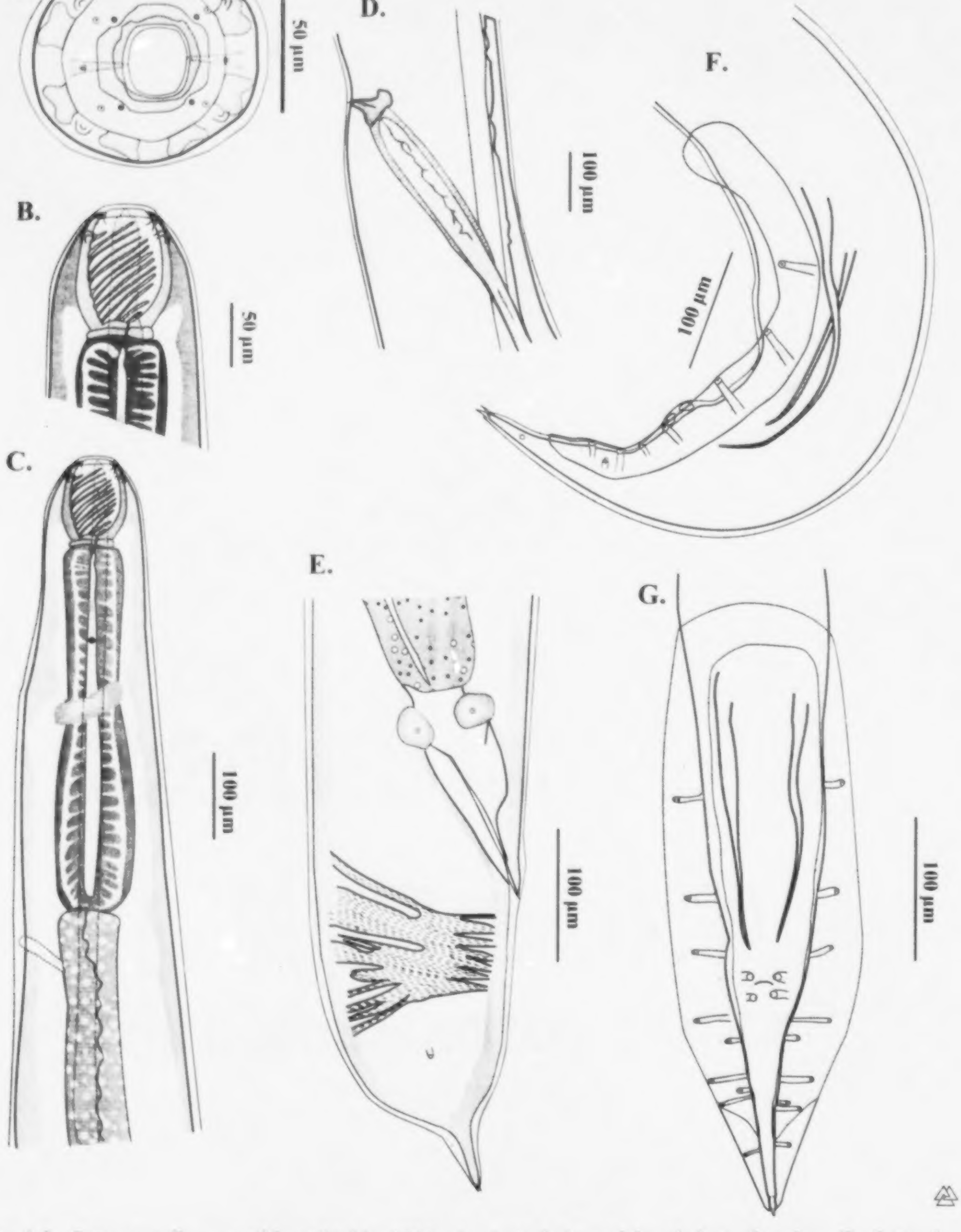
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Fig. 4-3. *Spirocamallanus istiblenni* Noble, 1966. A. Apical view of female buccal region. B. Lateral view female buccal region. C. Lateral view of female anterior end. D. Lateral view of vulva from a non-gravid female. E. Lateral view of female posterior end. F. Lateral view of male posterior end. G. Ventral view of male posterior end.

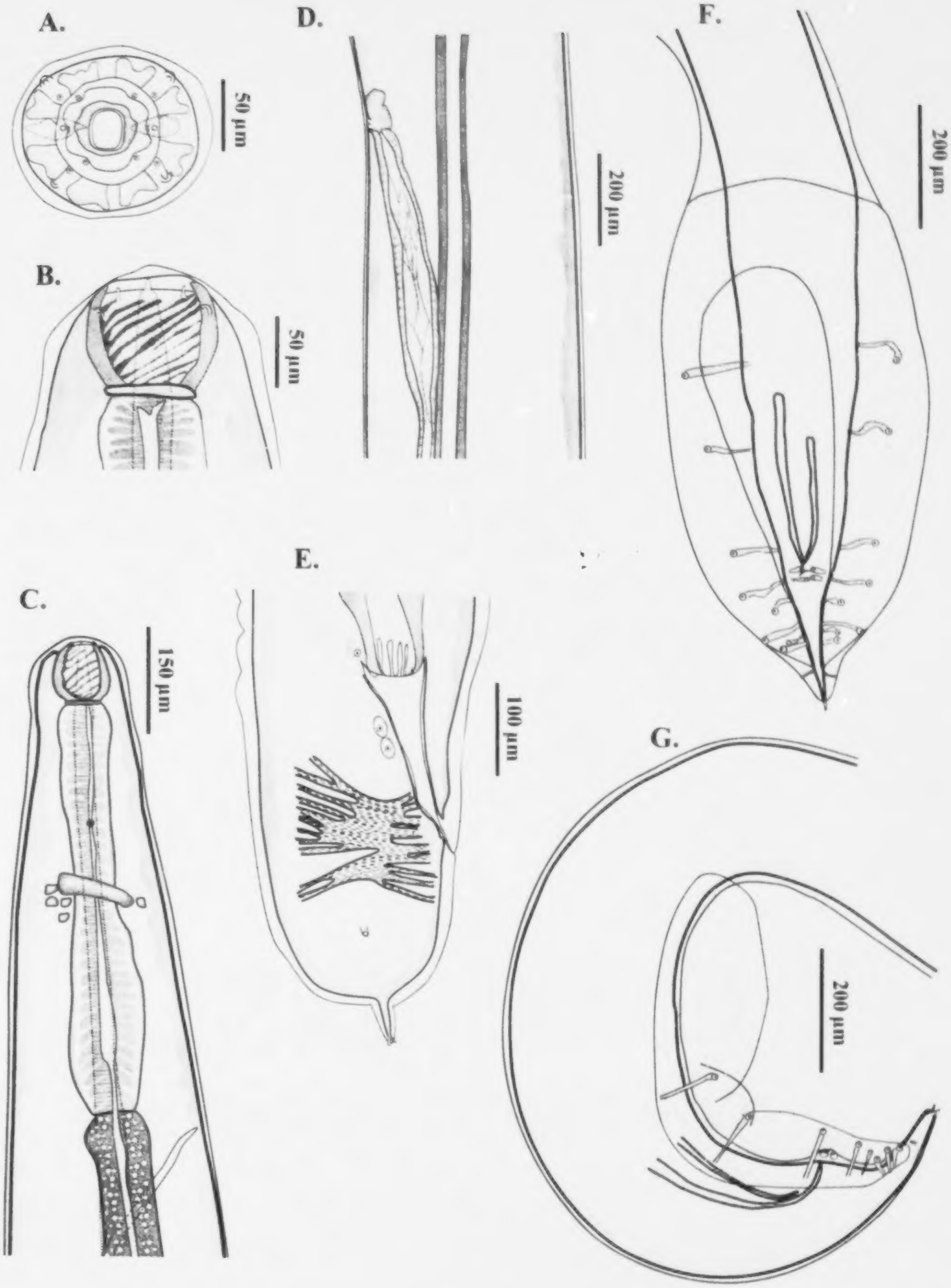
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Fig. 4-4. *Spirocamallanus monotaxis*. A. En face of female cephalic extremity. B. Lateral view female cephalic extremity. C. Lateral view of female esophageal region. D. Lateral view of vulva, uterus omitted for clarity. E. Lateral view of female caudal extremity. F. Ventral view of male caudal region. G. Lateral view of male caudal region.

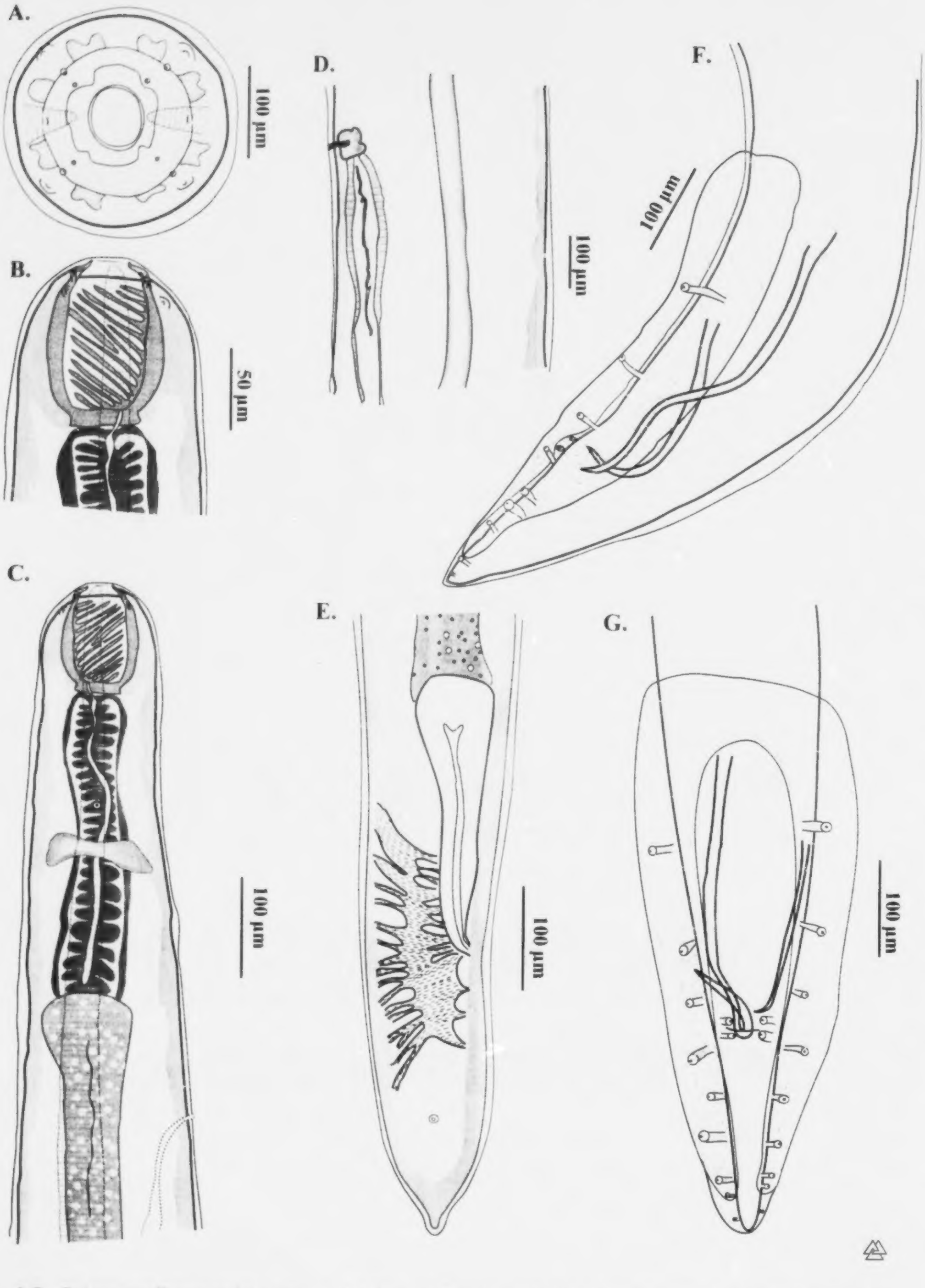
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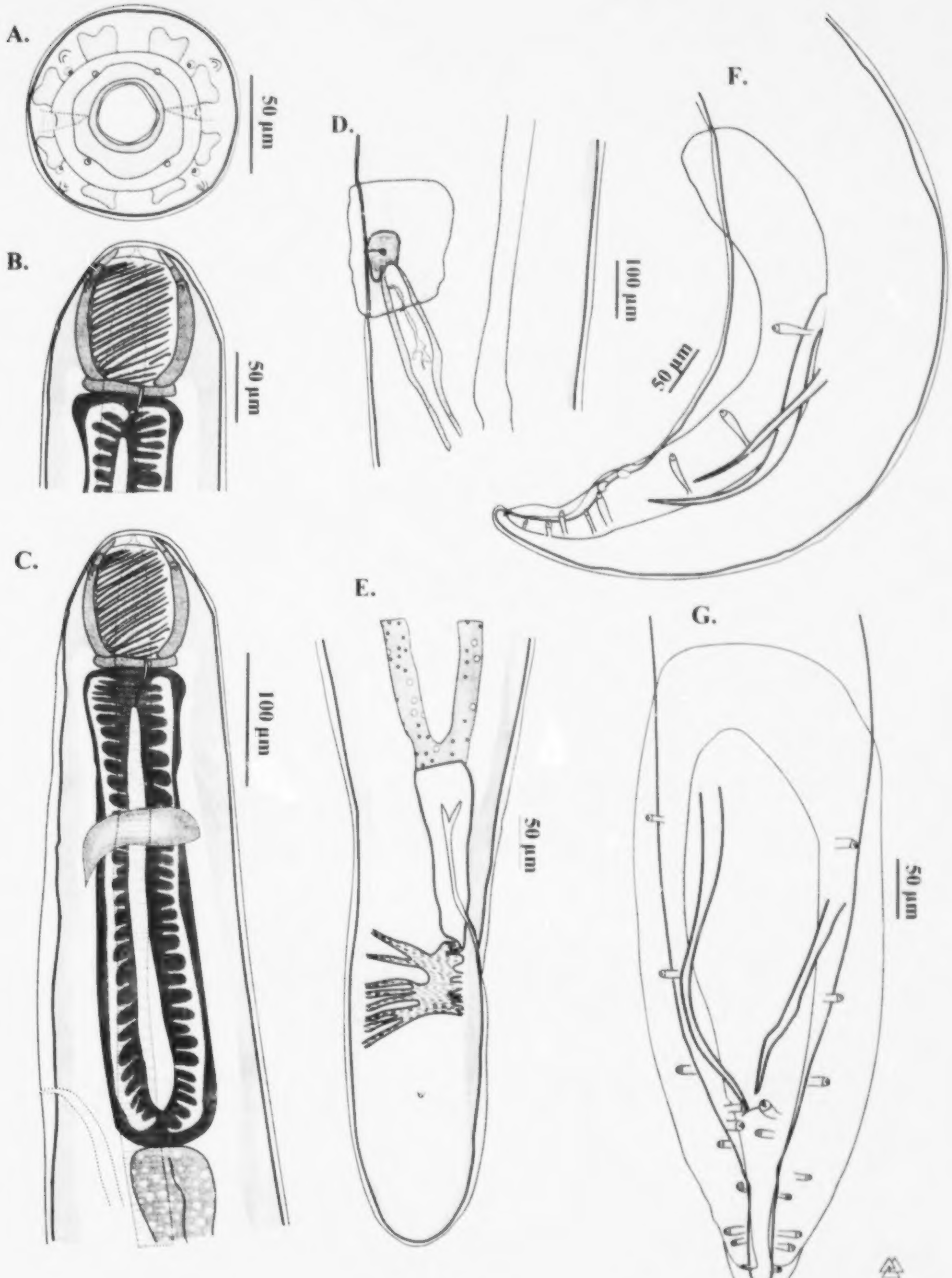
Fig. 4-5. *Spirocamallanus colei* n. sp. A. En face of female cephalic extremity. B. Lateral view female cephalic extremity. C. Lateral view of female esophageal region. D. Lateral view of vulva, uterus omitted for clarity. E. Lateral view of female caudal extremity. F. Lateral view of male caudal region. G. Ventral view of male caudal region.


A.
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G.
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Fig. 4-6. *Spirocamallanus chaimha* n. sp. A. En face of female cephalic extremity. B. Lateral view female cephalic extremity. C. Lateral view of female esophageal region. D. Lateral view of vulva, uterus omitted for clarity. E. Lateral view of female caudal extremity. F. Lateral view of male caudal region. G. Ventral view of male caudal region.

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5. General discussion and conclusions

The parasite community of honeycomb groupers in French Polynesia was low in both species diversity and numbers of individuals when compared to other marine fishes, and particularly, to china rockfish (Holmes 1990; Curran and Caira 1995) (Fig. 2-4). The poorly developed parasite community made some of my questions inappropriate, patterns at the smaller scales difficult to discern or demonstrate, and patterns at the larger scales more interesting.

The low number of species, and particularly the low prevalences and intensities, made questions at the infracommunity level inappropriate. Although patterns at this level may be discerned in data on species poor communities (e.g., Holmes and Bartoli 1993), discerning such patterns requires higher prevalences and intensities than in my data. The data, however, do clearly indicate that infracommunity "structure" is the result of recruitment limited community dynamics, not post-recruitment interactions (Booth and Brosnan 1995).

Patterns at smaller scales (i.e., within host populations, between habitats, locations on the same island, and islands in the same archipelago) in my data are difficult to discern. In some cases, even the absence of a parasite species from a sampling location was not diagnostic (see Chapter 2). Within host populations, the only clear difference in parasite community structure was the difference between recruiting fishes and adults. Growth in fishes, particularly in the smaller size classes, is often correlated with a change in diet (Werner 1986), with consequent changes in the parasite faunae. In the present system, encysted cestode larvae were lost by honeycomb groupers after recruitment (see Chapter 3). Honeycomb grouper larvae are planktivorous (Leis 1991), whereas adults consume benthic macrofaunae (Harmelin-Vivien and Bouchon 1976), thus exposing adults to a different suite of parasites than larvae. The difference in the parasite communities between the two age-classes would therefore seem to be the result of their change in diet rather than a size-related difference. The only size-related pattern found in adult honeycomb groupers was the increase in intensity of *Sc. polymorphus* with size (see Chapter 2; Fig. 2-2).

For the other smaller scales (between habitats and locations on the same island), the best indicator of pattern in my data would appear to be the mean numbers of parasite species and parasite individuals per fish (Table 2-1). This clearly shows that parasite community richness was greater on the barrier reef than on the fringing reef. Thus, parasite richness may be positively related to wave exposure, as was seen in china rockfish (Holmes unpublished data). The mean numbers of species and individuals per fish also indicate that different locations of the same habitat type on the same island have no obvious differences in parasite community structure, despite differences in fish faunae (Galzin 1987). Although logistic concerns ruled out the possibility, sampling in another, more different, location may have revealed greater within island differences.

For among island patterns within the same archipelago, Tetiaroa was sampled to test for differences between the parasite communities of atolls (Tetiaroa) and high islands (Moorea and Tahiti). However, the only area where I could sample honeycomb groupers was very similar to the barrier reefs of high islands. Additionally, sampling in less disturbed habitats would have been desirable as the parasite community there should be richer but the only area available on Tetiaroa had heavy siltation, lowering habitat quality.

Patterns at the larger scales are much more interesting. The adult helminths of honeycomb groupers found in the 2 archipelagos sampled in French Polynesia (the Society and the Tuamotu Islands) were different, but ecological equivalents. These differences do not appear to be the result of competitive exclusion as prevalences and intensities of the parasites were low (Table 2-1), leaving many vacant niches. For *Lecithochirium* spp., the difference in species between the 2 archipelagos may be rationalized by difficulties related to their life cycles (see Chapter 2); i.e., they, like most digeneans, should be highly specific to their molluscan intermediate hosts (Williams and Jones 1994), which may differ, and may not be present in both archipelagos. However, the differences in camallanid nematodes is not so easily explained. The camallanid nematodes from both locations appear to be found across the tropical Pacific, and *Sp. monotaxis* was present in other fishes in the Tuamotus (see Chapter 4). Because honeycomb groupers are not known to consume copepods (Harmelin-Vivien and Bouchon 1976), the only necessary intermediate host of worms of this group (Stromberg and Crites 1973), a paratenic host, or trophic bridge, is required. The same trophic bridges may not be available in both archipelagos, or the diets of honeycomb groupers may include different trophic bridges in the 2 archipelagos. Because of small sample sizes in the Tuamotus, the validity of these differences might be questioned. However, the ecologically equivalent parasites appear in approximately the same prevalences in both archipelagos, suggesting that the differences are real.

A cline in species diversity of digeneans is evident from my data from sampling locations across the south Pacific (Fig. 2-3). Unlike the differences between archipelagos, the added species are new and different species with different niches, not ecological equivalents. Additional species appear not only in the parasite community of honeycomb groupers, but also in other closely related serranids. The decreasing distance from the apparent species heartlands of both molluscs and coral-reef associated fishes, and increasing species diversity, to the west in the south Pacific (Kay 1980; Myers 1992), may in part produce this trend. Mollusc diversity is important to digeneans as they are generally highly specific to their molluscan first intermediate hosts (Williams and Jones 1994). In islands further to the east, where mollusc diversity is lower, the required molluscan intermediate hosts may be absent, thus adding to the difficulty of dispersing across the already large distances separating the islands in the south Pacific and preventing digeneans from successfully establishing. Diversity of fishes also decreases to the east across the south Pacific, which should lower the number of similar fish species. Parasites may be exchanged between similar hosts (e.g., Kennedy and Bush 1994; Chapter 4) and areas with more similar host species should provide more similar habitats for parasites. The greater number of available habitats, and the possibility of exchange between them, should result in a richer parasite fauna. Therefore, with increasing distance from a host species heartland, and the decrease in related host species, parasite diversity should decrease (Kennedy and Bush 1994). The parasite faunae of honeycomb groupers in the south Pacific appear to reflect this trend (Fig. 2-3). Were china rockfish sampled farther from their heartland, I would expect their parasite faunae to follow the same trend (i.e., to decrease).

The cline in species diversity seen in digeneans is not evident in camallanid nematodes of fishes in the south Pacific. Species diversity does not appear to decrease significantly from west to east (Fig. 5-1). While French Polynesia has a slightly greater diversity than elsewhere in the south Pacific, it is also the area with the greatest sampling effort for worms of this group (see Chapter 4; S. Morand et al. unpublished data). Worms of this family have a low specificity for their copepod intermediate hosts (Moravec et al. 1995), permitting them to infect a wide range of copepods. Thus, camallanid nematodes should be less sensitive to species gradients in their intermediate hosts across the south Pacific and better able to disperse than digeneans. The lack of a species cline in camallanid nematodes across the south Pacific may also be due to a potential use of pelagic hosts, including both pelagic copepods and fishes. Camallanid nematodes also appear to be able to infect some pelagic fishes (Chapter 4). This potential use of such pelagic hosts for both life history stages may enhance the dispersal ability of these worms.

Zoogeographic barriers to colonization can explain the low numbers of species found in honeycomb groupers, but not the low numbers of individuals of successful colonists. *Spirocamallanus* may have a life-history strategy in which a wide range of host species are infected, thus “spreading the risk”. This will reduce the number of individuals per host, but also lower the potential for competition (with both within the species and with other helminths) and enhance their colonization ability (i.e., they should be able to easily find a suitable host in most coral reef habitats). This should equally apply to *Camallanus* as they have also been found from a wide range of host species (e.g., see host records of *C. marinus* in Chapter 4). While other factors may be responsible for the low number of *Lecithochirium* individuals found, further work on the digeneans of French Polynesia may reveal a similarly broad host species range, implying a similar life-history strategy.

Overall, wheras the china rockfish parasite community appears to be well developed, that of honeycomb groupers of French Polynesia appears to be poor in species through zoogeographic barriers (i.e., low invasiveness due to isolation) and poor in individuals due to the life-history characteristics of the individual parasite species. The result is a parasite community in honeycomb groupers that is definitely recruitment limited.

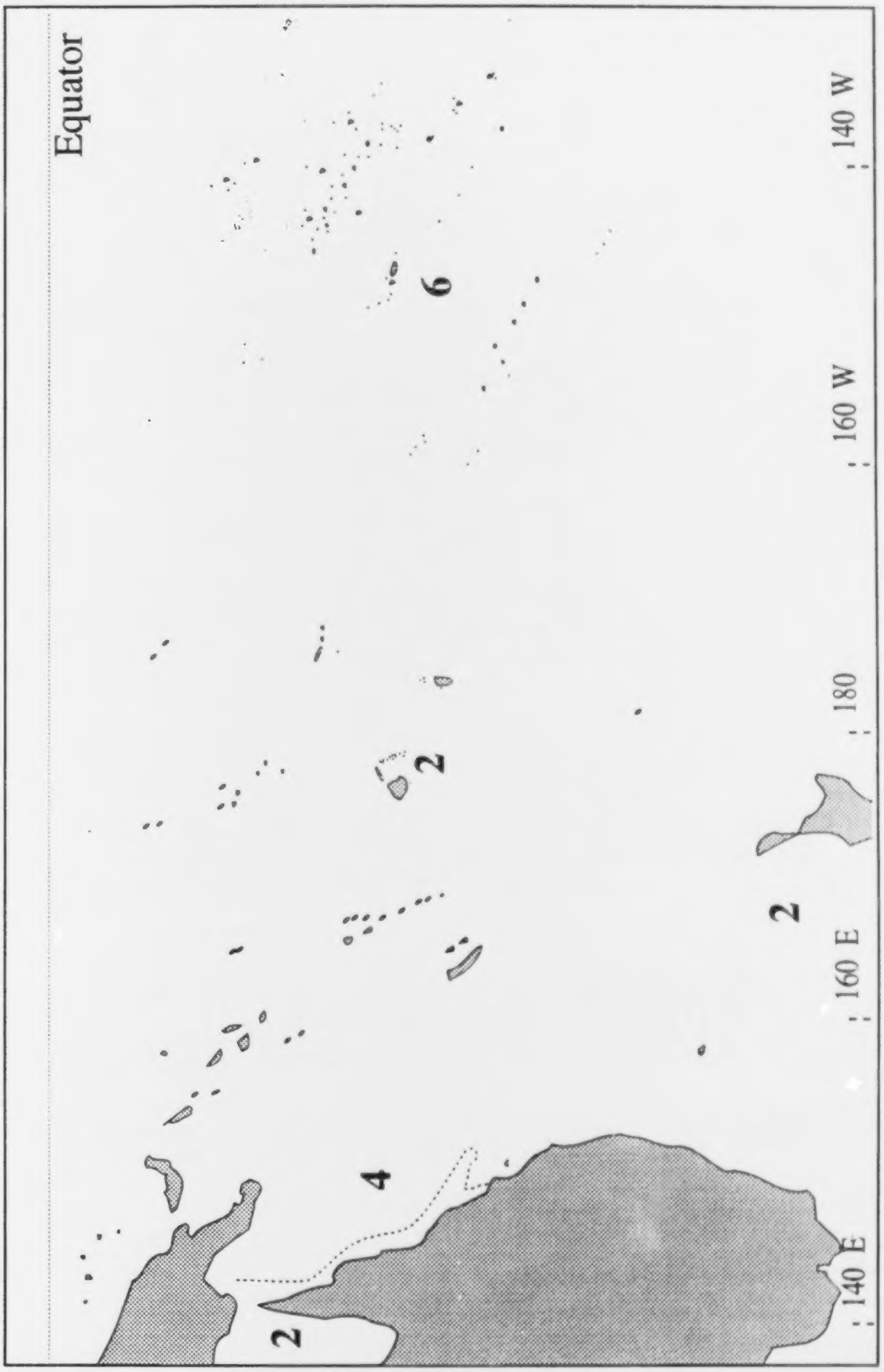
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Fig. 5-1. Number of species of camallanid nematodes reported from fishes in the south Pacific.

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